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A REVIEW OF THE WORLD RESOURCES OF MESOPELAGIC FISH

FOOD AND AGRICULTURE ORGANIZATION OF THE UNITED NATIONS

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by

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PREPARATION OF THIS PAPER

This review is part of a continuing effort by the Fishery Resources and Environment Division to provide current information on the potential and state of exploitation of the world's fishery resources, conventional and unconventional. Mesopelagic fish are hardly exploited at present, and there are a number of practical problems to be solved before they can be harvested commercially on a large scale, but their biological potential is large.

The authors of this paper collaborated in writing the introductory chspters on general topics (Ch. 1 - 4) and the concluding chapters (Ch. 21 and 22). Of the intervening area reviews, those covering the Atlantic Ocean and the western Indian Ocean were prepared by Dr. Gjøsaeter, and the rest by Dr. Kawaguchi.

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CONTENTS

		Page
1.	INTRODUCTION	1
2.	SYSTEMATICS	3
	2.1 Families of mesopelagic fishes	3
	2.2 Identification of myctophid fishes	3
	2.3 Identification of gonostomatid fishes	5
	2.4 The new classification for stomiatoid fishes	5
3.	ECOLOGY AND LIFE HISTORY	7
	3.1 Vertical distribution and migration	7
	3.2 Seasonal variation	7
	3.3 Horizontal distribution	7
	3.4 Behaviour	7
	3.5 Anatomy and physiology	11
	3.6 Position and importance in the food web	11
	3.7 Growth, mortality and production	14
	3.8 Fecundity	19
	3.9 Spawning seasons	22
	3.10 Life span and age at maturity	22
	3.11 Dwarf males, sex reversal and hermaphroditism	25
4.	METHODS OF ABUNDANCE ESTIMATION	27
	4.1 Net sampling	27
	4.2 Acoustic surveys	30
	4.3 Egg and larva surveys	31
5.	NORTHEAST ATLANTIC	33
6.	NORTHWEST ATLANTIC	41
7.	EASTERN CENTRAL ATLANTIC	47
8.	WESTERN CENTRAL ATLANTIC	53
9.	SOUTHEAST ATLANTIC	59
10.	SOUTHWEST ATLANTIC	61
11.	MEDITERRANEAN SEA	65
12.	WESTERN INDIAN OCEAN	71
13.	EASTERN INDIAN OCEAN	81
14.	NORTHWEST PACIFIC	87
15.	NORTHEAST PACIFIC	95
16.	WESTERN CENTRAL PACIFIC	101
17.	EASTERN CENTRAL PACIFIC	105

Page

18. SOUTHEAST PACIFIC 115

19. SOUTHWEST PACIFIC 117

20. THE ANTARCTIC 119

21. DISCUSSION OF FISHERY POTENTIAL 121

21.1 Summary abundance information 121
21.2 Potential yield 127
21.3 Species of potential commercial interest 128
21.4 Present catches 130

22. NEEDS FOR FUTURE STUDIES 133

23. REFERENCES 135

1. INTRODUCTION

During recent years an increasing proportion of conventional fish stocks has reached a state of full exploitation or even over-exploitation, and the search for new fishery resources has been intensified. At present, it seems that krill, cephalopods and mesopelagic fish are the most promising potential resources (Gulland, 1971; Okutani, 1977).

A fish species can be called mesopelagic if it spends the day in the mesopelagic zone. The mesopelagic zone has been defined in different ways based on depth, temperature and light regimes. For the present purpose, depth seems to be the best criterion and mesopelagic fish can thus be defined as species generally spending the day at depths between approximately 200 and 1 000 m. Generally they perform a diel migration, coming to the upper 200 m or even to the surface during the night.

Species of many fish families will fall within this definition, but generally the Myctophidae and Gonostomatidae are dominant. Sternoptychidae, Bathylagidae, Chiasmodontidae, Trichiuridae, Nomeidae and others seem to be fairly important in some areas. In this report the main emphasis will be placed on the Myctophidae and on the mesopelagic members of the family Gonostomatidae.

Mesopelagic fish are found in all oceans from the Arctic to the Antarctic, but the number of species and, in general, the annual production are highest in subtropical and tropical seas. Both typically oceanic and neretic species are found.

There are rather few examples of utilization of mesopelagic fish. The most well known is the purse seine fishery for *Lampanyctodes hectoris* off South Africa (Newman, 1977), but the fishing fleet of the U.S.S.R. are also fishing myctophids off West Africa, and off Southeast Australia mesopelagic fish (*Maurolicus muelleri* and *Lampanyctodes hectoris*) have been caught during exploratory fishing.

Fish meal and oil and fish silage have been produced, but some species (*Diaphus coeruleus* and *Gymnoscopelus nicholski*) have also been fished for human consumption (Melnikova, 1973; Dubrovskaya and Makorov, 1969). Other species seem to have adverse effects due to their high content of wax esters.

The bulk of early work on mesopelagic fish was concerned primarily with taxonomy and distribution. There are still many unsolved problems in these fields, but the recent literature has been mostly concerned with vertical distribution and migration and other aspects of the ecology of the group (e.g. Clark, 1973, 1974; Badcock and Merrett, 1976, 1977; Roe, 1974). The larvae of Myctophidae and Gonostomatidae have also been intensively studied during recent years (e.g. Moser and Ahlstrom, 1970, 1972, 1974 and Ahlstrom, 1974).

Knowledge about the food and feeding habits of mesopelagic fish has also increased and their importance as vertical transporters of organic matter has been stressed (e.g. Legand and Rivaton, 1969; Merrett and Roe, 1974; Hopkins and Baird, 1977). The literature gives a fairly clear picture of what mesopelagic fish eat, but it is less informative as to what eats mesopelagic fish.

Comprehensive data on the life history of any mesopelagic species is sparse. Age and growth are known for some of the more important cold-water species but only tentative information is available on tropical ones. The reproductive biology is still little known.

The present report briefly reviews the systematics, ecology and life history of important groups of mesopelagic fish. Further, some methods used for abundance estimation of these fish are described and discussed. The bulk of the report reviews the present knowledge of abundance and species composition of mesopelagic fish in each of the FAO statistical areas. Although the data in most cases are few, an attempt has been made to give tentative estimates of the biomass and production in the various areas. When available, information on the life history of the most important species in each area is also given.

2. SYSTEMATICS

2.1 Families of mesopelagic fishes

Beneath the epipelagic zone, fishes belonging to about 100 families have been known to occur. Of these, 73 families are the so-called "oceanic deep-water fishes" and the other 26 are "secondary deep-water fishes" (Rass, 1967). The fishes of the mesopelagic zone are mostly oceanic deep-water fishes and belong to about 30 families, although members of some families occur also in the epipelagic and bathypelagic zones (Rass, 1967; Parin, 1968).

The families of mesopelagic fishes are listed in Table 2.1, with the number of genera in each family, based on Lindberg (1971). The number of families and genera, and their arrangement, are different in the various classification systems (Berg, 1940; Greenwood *et al.*, 1966; Gosline, 1971). However, the aim of this report is not to present a detailed systematic account. Based on the number of genera in each family, the fishes of the families Gonostomatidae (20 genera), Melanostomiatidae (15), Myctophidae (30), and Gempylidae (20) are the most diverse at the generic level. Of these, fishes of the Myctophidae and Gonostomatidae account for 60 - 90 percent of the total catch of micronektonic fishes, both in weight and number, and are thus the most important groups from both the taxonomical and ecological point of view.

2.2 Identification of myctophid fishes

The identification of myctophid fishes has been difficult due to taxonomic confusion. Recently such confusion has been gradually reduced as some comprehensive keys to species have become available for some or most of the genera in certain areas. But the amount of study has been very uneven among areas and genera, and the more recent works have always complemented the older ones.

Here we shall only refer to comprehensive works presenting good descriptions and keys to species, which were contributed to journals or books easily available even to people unfamiliar with myctophid taxonomy. Considering the great number of species, of which some are cosmopolitan and others are endemic to only some areas, we shall deal with this family ocean by ocean.

Atlantic Ocean: Knowledge of the myctophid fauna is well advanced in the North Atlantic Ocean. For identification of the 82 North Atlantic species, the description and keys by Nafpaktitis *et al.*, (1977) are the most comprehensive. Kreft and Bekker (1973) have prepared a checklist of 57 species in the eastern North Atlantic, north of 30°N, and the Mediterranean. All of these 57 species are included in the keys of Nafpaktitis *et al.*, (1977), with the exception of one species, *Ctenoscopelus phengodes* (Lütken, 1892), whose occurrence is based on a single specimen reported by Zugmayer (1911) and is doubtful. The South Atlantic Ocean shares many species with the North Atlantic (Nafpaktitis *et al.*, 1977). However, a comparison of the species lists of the North and South Atlantic (Nafpaktitis *et al.*, 1977; Parin *et al.*, 1974; Kreft, 1974) suggests that at least 30 species of 14 genera, which are not distributed in the North Atlantic, occur in the South Atlantic. Most of these species have a circumpolar distribution in the southern hemisphere. Therefore, for the identification of these species, it is advisable to use the keys and/or descriptions of the species in the Indian Ocean (Nafpaktitis and Nafpaktitis, 1969; Nafpaktitis, 1978) and in the eastern Pacific (Wisner, 1976) in combination with those of Nafpaktitis *et al.*, (1977). It should be noted that considerable improvement and changes in genus and species names are found in Nafpaktitis (1978).

Indian Ocean: For the identification of the species of *Diaphus* the description of 36 species by Nafpaktitis (1978) is the most up-to-date and comprehensive. For the fishes of other genera, the description of 54 species by Nafpaktitis and Nafpaktitis (1969) and Kotthaus (1972) are helpful, although their sampling coverage is restricted to the western Indian Ocean. The species of the genera *Protomyctophum* and *Electrona* show a circumpolar distribution in the antarctic region and some of them do not occur in the sampling areas of the above two works. But they are included in the keys for the eastern Pacific myctophids by Wisner (1976)

owing to their circumpolar distribution. Generally, faunal surveys have not been adequate in the eastern and southern Indian Ocean and more taxonomical study is needed in the genera *Lampanyctus*, *Symbolophorus* and *Gymnoscopelus* to establish the identification of the Indian Ocean myctophid fishes.

Pacific Ocean: Wisner (1976) compiled available information on the taxonomy and distribution of 147 species of the eastern Pacific. His keys to these species are helpful in identifying not only the eastern Pacific species, but also the species of the central and western Pacific and the Indian Ocean. He noted that the key is a preliminary one and incomplete in regard to the genera *Diaphus*, *Gymnoscopelus* and *Lampanyctus*. Bekker (1964, 1965) and Bekker and Borodulina (1976) studied the taxonomy and distribution of the slender-tailed myctophids, *Loweina*, *Tarlentonbeania*, *Gonichthys*, *Centrobranchus*, *Hygophum* and *Myctophum* in the entire Pacific and Indian Oceans. In the western Pacific, Kawaguchi and Aioi (1972) studied the taxonomy and prepared a key to the species of *Myctophum*. Kawaguchi and Shimizu (1978) did the same for *Diaphus* in the eastern Indian Ocean, the Southeast Asian Seas and the western Pacific.

Table 2.1

Families of fishes occurring in the mesopelagic zone
(based on Lindberg, 1971)

Families	Number of genera	Families	Number of genera
Argentinidaea	2	Alepisauridae	1
Bathylagidae	2	Scopelarchidae	5
Opisthoproctidae	4	Evermannellidae	3
Gonostomatidae	20	Giganturidae	2
Sternoptychidae	3	Nemichthyidae	ca. 5
Stomiatidae	2	Trachypteridae	3
Chauliodontidae	1	Regalecidae	2
Astronesthidae	6	Lophotidae	2
Melanostomiatidae	ca. 15	Melamphaeidae	2
Malacosteidae	4	Anoplogasteridae	2
Idiacanthidae	1	Chiasmodontidae	5
Myctophidae	ca. 30	Gempylidae	20
Paralepididae	5	Trichiuridae	8
Omosudidae	1	Centrolophidae	1
Anotopteridae	1	Tetragonuridae	1

Generally, the taxonomy of the Pacific myctophids is not yet complete especially in regard to the genera *Lampanyctus*, *Gymnoscopelus* and *Diaphus*, and more faunal survey is needed in the central South Pacific and the Southeast Asian Seas. But studies on the myctophid fishes of Australia, the Southeast Asian Seas, New Caledonia and the western tropical Pacific have made steady progress and are nearing completion (pers. comm. B.G. Nafpaktitis and J.R. Paxton). These studies will certainly contribute to understanding of the taxonomy and distribution of the myctophids in the entire Pacific and world oceans as well.

2.3 Identification of gonostomatid fishes

The taxonomy of gonostomatid fishes is more developed than that of myctophids. The backbone of the taxonomy at the generic level was established by Grey (1960, 1964) and was not significantly changed until Weitzman (1974) proposed a new evolutionary classification (Table 2.2). For convenience, we follow Grey's system, since most previous works have followed it. Twenty-one genera are included in her key to the genera of the world oceans, although the genus *Neophos* was later synonymized with *Torophos* by Weitzman (1974). At present, the total number of gonostomatid genera is 20 as shown in Table 2.2. Of these 20 genera, *Yarrella*, *Polymetme* and *Argripnus* have been collected by bottom trawl and are not thought to be meso- or bathypelagic, while fishes of the other 17 genera are. Of the 17 genera, *Cyclothone* with 11 species and *Gonostoma* with 7 species are the largest, while seven genera, *Triplophos*, *Pollichthys*, *Photichthys*, *Bonapartia*, *Margrethia*, *Denaphos* and *Maourolicus*, are monotypic. *Diplophos* and *Vinciguerria* include four species, *Ichthyococcus* and *Valenciennellus* three species and *Woodsia*, *Thorophos*, *Araiophos* and *Sonoda* two each.

For identification at both the generic and species level, Grey's (1960, 1964) keys and descriptions are still helpful, although her description is restricted to northwest Atlantic species, and the keys are not prepared to deal with some taxonomically confused genera such as *Cyclothone* and *Diplophos*. But most of this confusion has been recently resolved and their distributions have been clarified by Berry and Perkins (1966), Mukhacheva (1967, 1972, 1974, 1976), Kawaguchi (1971) and Kobayashi (1973), who give comprehensive descriptions and keys to species of a specific area or the world oceans. Several species new to science were also described during the last decade, i.e., *Araiophos eastropas* Ahlstrom and Moser, 1969; *Diplophos greyae* Johnson, 1970; *Diplophos rebainsi* Kreft and Parin, 1972; *Woodsia meyerwaardeni* Kreft, 1973; *Gonostoma longipinnis* Mukbacheva, 1972; *Cyclothone sumiae* Kabayashi, 1973. Recent advances in gonostomatid taxonomy are well reflected in the description of these species.

2.4 The new classification for stomiatoid fishes

Recently Weitzman (1974) proposed a new classification for stomiatoid families based on their osteology. His classification resulted in considerable changes in the arrangement of genera. He transferred seven genera from Gonostomatidae to Photichthyidae, which he newly established, and seven genera from Gonostomatidae to Sternoptychidae, which had formerly included only the three genera *Polyipnus*, *Argyropelecus* and *Sternoptyx* as shown in Table 2.2. In his classification, Sternoptychidae and Photichthydae are given high rank together with Gonostomatidae and Myctophidae as families with abundant micronektonic fishes. We compare his system to the older one in Table 2.2, since many workers may adopt his system in the near future and some confusion may occur among workers unfamiliar with stomiatoid taxonomy over the definition of the families Gonostomatidae, Sternoptychidae, and Photichthyidae.

Table 2.2

Comparison of the classification systems of Grey (1960, 1964) and Weitzman (1974)

Grey (1960, 1964)	Weitzman (1974)
Gonostomatidae (20 genera)	Gonostomatidae
1. *Diplophos* Gunther	(6 genera)
2. *Triplophos* Brauer	
3. *Bonapartia* Goode and Bean	
4. *Margrethia* Jespersen and Tåning	
5. *Gonostoma* Rafinesque	
6. *Cyclothone* Goode and Bean	
7. *Thorophos* Bruun*	Sternoptychidae
8. *Araiophos* Grey	(10 genera including
9. *Maurolicus* Cocco	*Polyipnus* Cocco
10. *Danaphos* Bruun	*Argyropelecus* Gunther
11. *Valenciennellus* Jordan and Evermann	*Sternoptyx* Herman
12. *Argyripnus* Gibert and Cramer	
13. *Sonoda* Grey	
14. *Vinciguerria* Jordan and Evermann	Photichthyidae
	(7 genera)
15. *Polymetme* McCulloch	
16. *Yarrella* Goode and Bean	
17. *Pollichthys* Grey	
18. *Photichthys* Grey	
19. *Woodsia* Grey	
20. *Ichthyococcus* Bonaparte	

* Including *Neophos* Myers

3. ECOLOGY AND LIFE HISTORY

3.1 Vertical distribution and migration

An extensive diel vertical migration is one of the most striking features of most mesopelagic fish species. During the day most fish are concentrated in one to several deep scattering layers (DSL) found at depths from about 200 m downwards (Fig. 3.1), but net sampling and direct observations from bathyscaphes have both indicated that mesopelagic fish can also be found between these layers (Bradbury *et al.*, 1971; Barham, 1971). Light seems to be a major factor regulating the depth of the DSL (Kampa, 1971) (Fig. 3.2), and particular species often seem to follow particular isolumes during migration (Boden and Kampa, 1967; Clarke, 1971). During nighttime some species (e.g., many myctophid genera) come to the surface layer, while others stop at intermediate depths, or do not migrate at all (Pearcy and Laurs, 1966; Badcock and Merrett, 1976). Some authors (e.g., Gorelova, 1977) classify the surface migrating forms as *nictoepipelagic* and those spending all the time within the mesopelagic zone as *mesopelagic*. There also seems to be some ontogenetical variation in migration habits (Nafpaktitis, 1968; Clarke 1973, 1974) and there are indications that some fish migrate to the upper layers some nights while they stay at depth other nights (Clarke, 1971). Usually the fish are most concentrated when in the DSL during the day (Taylor, 1968), but very dense concentrations have also been observed in the surface layer during the night (Gjøsaeter, 1978a). There are also a few observations of myctophids coming to the surface during daytime (Alverson 1961), but this phenomenon seems to be of no general importance.

3.2 Seasonal variation

Data related to seasonal variation are few and partly contradictory. Haigh (1971) and Ponomareva (1974) found only negligible seasonal variation during acoustical studies of DSLs, while Donaldson and Pearcy (1972) found more pronounced variation. The reproduction of mesopelagic fish shows a seasonal variation even in tropical and subtropical waters, and associated with this, variation has also been observed in both size distribution and biomass of individual species and of the total mesopelagic assemblage (Gibbs *et al.*, 1971; Clarke, 1973). In temperate waters seasonal variations have also been observed (Pearcy, 1977).

3.3 Horizontal distribution

The distributional patterns of mesopelagic fish generally seem to coincide with water mass distribution (Cohen, 1973). Some species have a restricted area of distribution, while others are found in all oceans. Most mesopelagic fish are oceanic, but neritic distributions have also been observed (e.g., Clarke 1973).

The horizontal distribution of biomass depends on production at lower trophic levels (Blackburn, 1977), and also on local factors. Off Oregon, Pearcy (1976) found the highest biomass about 45 nautical miles offshore, while Gjøsaeter and Blindheim (1978) observed the highest biomass of mesopelagic fish a few miles off the 200 m depth contour off Northwest Africa (Fig. 3.3).

There are few indications of horizontal migration among mesopelagic fish, and special feeding or spawning concentrations have not been reported. The larval distribution (e.g., Ahlstrom, 1972) seems to support the hypothesis of no spawning migration. It has, however, been suggested that mesopelagic fish may be expatriated in areas with strong currents (O'Day and Nafpaktitis, 1967; Zurbrigg and Scott, 1972; Gjøsaeter, 1978). These expatriated specimens are probably lost to the reproductive part of the population.

3.4 Behaviour

Aspects of the behaviour of mesopelagic fish have been observed by means of trawls, acoustic instruments and submersibles. Some species may be found in schools, or aggregated in scattering layers, or dispersed (Pearcy and Laurs, 1966; Backus *et al.*, 1968; Gjøsaeter, 1978a).

Figure 3.1 Echo recording showing vertical migration of mesopelagic fish off West Africa, November 1972. (From Gjøsaeter and Blindheim , 1978)

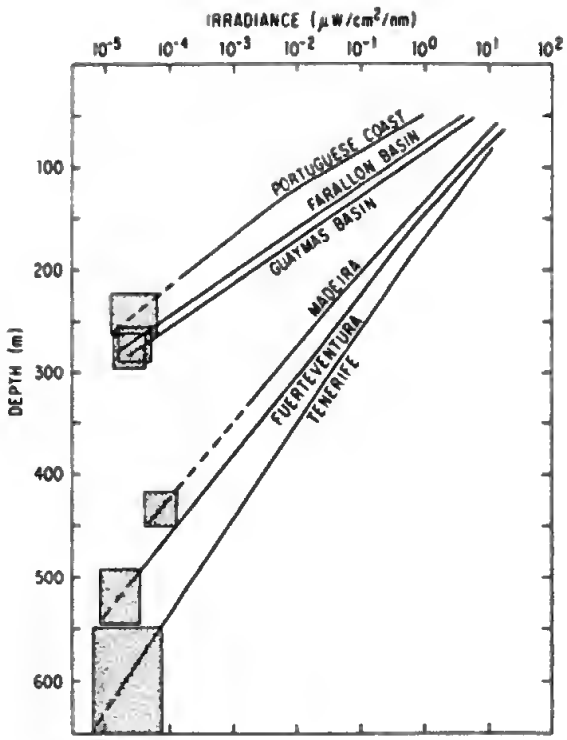

Figure 3.2 Relationships between irradiance at 480 nm throughout the water column and midday depth of a DSL in some regions of the eastern north Atlantic and the Gulf of California. Stippled areas indicate vertical extent of DSLs. (From Kampa, 1971)

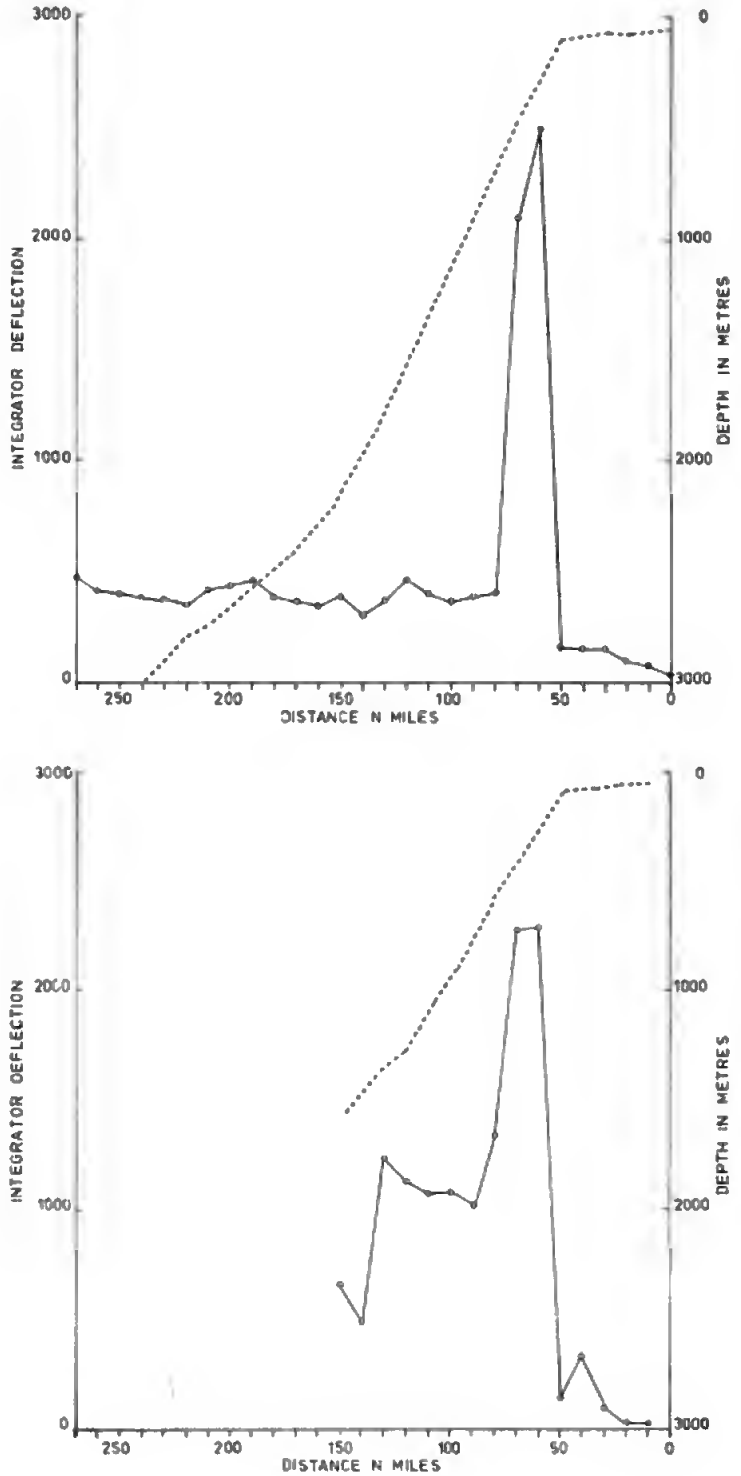

Figure 3.3 Integrated echo intensities refer to mesopelagic fish showing concentrations of fish near the shelf break off West Africa, November 1972. (From Gjøsaeter and Blindheim, 1978)

During daytime Barham (1971) often observed mesopelagic fish hanging motionless in the water with head up or down, apparently in a state of torpor. During night the fish in the upper layers were active, swimming horizontally, while fish staying at depth often were observed to be immobile and vertically oriented. The torpid fish were, however, capable of rapid evasive movements when approached by the submersible.

The ability to avoid nets depends on behaviour and on the efficiency of the sensory organs. Both surface and underwater observations show that the myctophids are capable of rapid swimming when attacked by predators, but they seem soon to become exhausted. The possibility of avoiding a net is dependent on orientation relative to the path of the net (Harrison, 1967; Scully-Power, 1977). Therefore the vertical position often observed during daytime may partly explain the better catches made during the night than during the day (Pearcy and Laurs, 1966). Barham (1971) also suggested that fish actively swimming to feed or to avoid predators may be nearer the exhaustion point than those resting inactively, and therefore less able to avoid the net.

3.5 Anatomy and physiology

Except for features directly linked to classification, and the swimbladder, anatomical and physiological studies on mesopelagic fish are few (Jollie, 1954; Paxton, 1972; Weitzman, 1974). The swimbladder has been more intensively studied as it is of primary importance to the sound reflecting properties of these fishes. Many species, especially among the deepest-living forms, have no swimbladder (Marshall, 1960). Other species have a gas-filled swimbladder when young which becomes filled with fat in older age, and it has even been observed that among fish apparently of the same species, age and sex, and caught in the same area at the same time of the year, individuals with either fat-filled or gas-filled swimbladders may be found (Butler and Pearcy, 1972).

Most species, at least among those inhabiting the upper part of the mesopelagic zone, have gas-filled swimbladders. The size of these bladders determines the acoustic properties of the fish. Brooks (1977) recently studied the size of the swimbladder in 55 mesopelagic fish species. He observed large intra- and interspecific variation, but in general the bladder size was smaller than the 5 percent of body volume commonly assumed. His values were also considerably smaller than those observed by Shearer (1971). Differences in methods may be partly responsible for this discrepancy.

Various aspects of the physiology of mesopelagic organisms were recently reviewed by Childress (1977). Fat content and fat composition have been studied in a few mesopelagic fish species (Table 3.1). The results indicate extensive variation among species. A high content of wax esters seems to be common (Nevenzel *et al.*, 1969), and this may be an obstacle to utilizing these fish for human consumption (Kinumaki *et al.*, 1977).

3.6 Position and importance in the food web

Mesopelagic fish constitute a major part of the biomass in oceanic areas (Ahlstrom, 1969; Clarke, 1973). Yet their position in the food web is poorly understood. Data on the food of mesopelagic fish have accumulated and were recently reviewed by Hopkins and Baird (1977). Crustacea appear to be the principal forage (Table 3.2) with copepods, euphausiids, ostracods, amphipods and small decapods being the most important items. In addition to species variation, ontogenetic, seasonal and regional variation is observed (Gjøsaeter,1973b; Hopkins and Baird, 1973; Gorlova, 1974; Tyler and Pearcy, 1975). Generally it seems that most mesopelagic fish are opportunistic feeders, consuming any available food falling within the size limits which they can manage. Exceptions are, however, observed (Table 3.2). The prey taken is partly herbivorous and partly carnivorous. Some studies indicate that herbivorous plankton dominate (Legand and Rivaton, 1969; Baird *et al.*, 1975), but the data available are too sparse to assess the relative importance of these components for most mesopelagic species.

Table 3.1
Lipid content of some mesopelagic fishes
with percentage of wax content in total lipids

Species	Lipid in fresh body wt. (%)	Wax ester in total lipid (%)	Author
Gonostomatidae			
Cyclothone atraria	4.0	58.4	Kayama and Ikeda, 1975
C. pseudopallida	4.3	53.5	Kayama and Ikeda, 1975
C. alba	5.3	54.0	Kayama and Ikeda, 1975
C. pallida	2.3	34.0	Kayama and Ikeda, 1975
Gonostoma gracile (♀)	2.5	20.0	Kayama and Ikeda, 1975
G. gracile (♂)	2.9	15.9	Kayama and Ikeda, 1975
Maurolicus muelleri	5.5	15.3	Kayama and Ikeda, 1975
M. muelleri (silage)	3.1		Anon, 1977a
Myctophidae			
Benthosema pterotum	4.6		B. Myrseth (in prep.)
Hygophum reinhardti	3.3	10	Nevenzel *et al.*, 1969
Myctophum nitidulum	3.8	10.6	Kayama and Ikeda, 1975
*M. asperum**	2.0	17.2	Kayama and Ikeda, 1975
Symblophorus evermanni	3.1	10	Nevenzel *et al.*, 1969
S. californiensis	4.3	trace	Nevenzel *et al.*, 1969
Tarletonbeania crenularis	2.1	5 (max.)	Nevenzel *et al.*, 1969
Diaphus theta	15.8	trace	Nevenzel *et al.*, 1969
D. coeruleus	10.2-17.2		Melnikova, 1973
D. glandulifer (= *D. suborbitalis*)	7.9	3.7	Kayama and Ikeda, 1975
*D. fulgens** (= *D. kuroshio*)	7.1	4.4	Kayama and Ikeda, 1975
D. latus (= *D. garmanni*)	8.7	1.7	Kayama and Ikeda, 1975
*Stenobrachius nannochir**	11.4	67.1	
S. leucopsarus	15.6	90.9	Nevenzel *et al.*, 1969
Triphoturus mexicanus	14.5	82.2	Nevenzel *et al.*, 1969
Lampanyctus ritteri	14.2	58	Nevenzel *et al.*, 1969
L. macropterus	11.9	3.7	Kayama and Ikeda, 1975
Lampanyctodes hectoris	20	no data	Centurier-Harris, 1974
Sternoptychidae			
*Sternoptyx diaphana**	1.4	4.2	Kayama and Ikeda, 1975
Chauliodontidae			
*Chauliodus sloani**	2.4	7.2	Kayama and Ikeda, 1975

* Excluding head. In other species not asterisked, whole fish was examined.

Table 3.2

Feeding behaviour of some mesopelagic fishes

Species	Area	Time of Feeding	Selectivity	Author
Myctophum spinosum	W. Equatorial Pacific	night		Gorelova, 1974
M. aurolaternatum	-	night		Gorelova, 1974
Sympolophorus evermanni	-	night		Gorelova, 1974
Benthosema glaciale	Norwegian fjords	night	random	Gjøsaeter, 1973
Benthosema glaciale	N.W. Africa	night		Kinzer, 1977
B. pterotum	Arabian Sea	evening/ night	?random	Gjøsaeter, 1978a
B. fibulatum	-	evening/ night		Gjøsaeter, 1978a
Diaphus taaningi	Off Venezuela	night		Baird *et al.*, 1975
D. theta	Off Oregon coast	night/ morning		Tyler and Pearcy, 1975
D. dumerili	N.W. Africa	acyclic		Samyshev and Schetinkin, 1971
Lobianchia dofleini	N.E. Atlantic	night	random	Merrett and Roe, 1974
Notolychnus valdiviae	N.E. Atlantic	night	?selective copepods	Merrett and Roe, 1974
Stenobrachius leucopsarus	Off Oregon coast	night/ morning		Tyler and Pearcy, 1975
Tarletonbeania crenularis	Off Oregon coast	night/ morning		Tyler and Pearcy, 1975
Lampanyctus cupriarius	N.E. Atlantic	night	selective amphipods	Merrett and Roe, 1974
Lepidophanes guentheri	N.W. Africa	acyclic		Samyshev and Schetinkin, 1971
Cyclothone acclinidens	Off California	night		De Witt and Calliet, 1972
Cyclothone signata	Off California	acyclic		De Witt and Calliet, 1972
Valenciennellus tripunctulatus	N.E. Atlantic	night	selective copepods	Merrett and Roe, 1974
Maurolicus muelleri	N.W. Africa	acyclic		Samyshev and Schetinkin, 1971
Argyropelecus aculeatus	N.E. Atlantic	dusk	selective ostracods	Merrett and Roe, 1974
A. hemigymnus	N.E. Atlantic	dusk	random	Merrett and Roe, 1974
Leuroglossus stilibius	Off California	night		De Witt and Calliet, 1972

The time of feeding by some species is shown in Table 3.2. Diurnal feeders, nocturnal feeders and acyclic feeders have been found.

Mesopelagic fish seem to partition food among themselves by species and ontogenetic variation in depth distribution and feeding time (Legand *et al.*, 1972; Kawaguchi, 1973; Merrett and Roe, 1974; Clarke, 1973, 1974). Differences in breeding season (Gibbs *et al.*, 1971; Goodyear *et al.*, 1972) may also lead to a partitioning of food between the younger stages.

It is very difficult to assess the daily ration of food consumed as the digestion rates are not known. If it is assumed that the stomach is filled once every night in cyclic feeders, data on stomach contents might be used to get an idea of food consumption. Baird *et al.*, (1975) found a maximum gut content of about 0.8% of the body weight of *Diaphus taaningi*, and Legand and Rivaton (1969) found similar percentages for various tropical myctophids.

There are many observations of various species of fish and other marine animals feeding on mesopelagic fish (see Table 3.3), but the importance of mesopelagic fishes in the diet of these animals is not clear.

Most commercial fish species feed above the shelf where mesopelagic fish species are not usually found. When they meet at the shelf edge there are examples showing that mesopelagic fish may be an important food item (e.g. Pereyra *et al.*, 1969).

There is some conflicting evidence about tuna feeding on mesopelagic fish. Legand *et al.*, (1972) and Roger and Grandperrin (1976) conclude that mesopelagic fish is of no importance as food for tuna. Others (see Table 3.3) have found that they may be a significant component in the diet of tuna species. It has also been shown that swordfish may eat mesopelagic fish although volumetrically they are of small importance (Scott and Tibbo, 1968).

Borodulina (1972) has shown that Chauliodontidae, Stomiatidae and various other deep-water predatory fish feed on Myctophidae and Gonostomatidae, while Fourmanoir (1969) concluded that *Alepisaurus* usually does not.

Several authors (e.g. Fitch and Brownell, 1968; Mead and Taylor, 1953) have shown that marine mammals may feed on mesopelagic fish, and for some species they may be an important part of the diet.

Cephalopods are another group of mesopelagic fish predators (e.g. Zuev and Nesis, 1971) and in some areas they may be the most important group.

3.7 Growth, mortality and production

Length distributions have been reported for a number of mesopelagic fish (e.g. Tåning, 1918; Gibbs *et al.*, 1971; Krueger and Bond, 1972; Goodyear *et al.*, 1972; Clarke, 1973,1974), but although a size distribution can sometimes be interpreted in terms of age, age is usually unknown, so the growth schedule cannot be determined. For mesopelagic fish inhabiting cold or temperate waters age can be read from the otoliths and growth can therefore be calculated. The growth of some of these species is shown in Table 3.4. The range in the growth coefficient, K, from the von Bertalanffy equation

$$l_t = L_\infty \left(1 - \exp\left[- K (t-t_o) \right]\right)$$

for the non-tropical species is 0.11 - 1.05 and the theoretical maximum lengths, L_∞ range between 49 and 119 mm. The data for *Benthosema glaciale* show that the growth parameters may vary extensively even within the same species and in the same general area. Typical growth curves are shown in Fig. 3.4.

Table 3.3

Some studies of animals feeding on mesopelagic fish

Predator	Area	Author
Oncorhyncus sp.	Off Wsshington	Shimada, 1948
Oncorhyncus sp.	N.E. Pacific	Manzer, 1968
Gadus morhua	Newfoundland	Popova, 1963
Gadus morhua	Newfoundland	Kashintsev, 1963
Sebastes marinus	Newfoundland	Kashintsev, 1963
Sebastodes flavidus	Off Oregon	Pereyra *et al.*, 1969
Sebastodes sp.	Off California	Fitch, 1951
Trachurus symonetricus	Off California	Fitch, 1951
Thunnus alalunga	Off California	McHugh, 1952
Thunnus alalunga	Off California	Pinkas *et al.*, 1971
Thunnus albacares	E. Tropical Pacific	Alverson, 1963
Katsuwonus pelamis	E. Tropical Pacific	Alverson, 1963
Thunnus thynnus	Off California	Pinkas *et al.*, 1971
Xiphias gladius	N.W. Atlantic	Scott and Tibbo, 1968
Scomber japonicus	Japan Sea	Nishimura, 1959
Glossanodon semifasciatus	Japan Sea	Okiyama, 1971
Theragra chalcogramma	Japan Sea	Nishimura, 1960
Arctoscopus japonicus	Japan Sea	Okiyama, 1971
Todarodes pacificus	Japan Sea	Okiyama, 1965
Stenella caeruleoalba	Off Central Japan	Miyazaki *et al.*,1973
Various cetacea	-	Fitch and Brownell, 1968
Callorhinus ursinus	Off Northern Japan	Jap.Fish.Agency, 1965

For tropical species, age determination is still tentative. Rings on the otoliths, supposed to be formed daily, have been used to age various shallow-water species (Panella, 1974; Brothers *et al.*, 1976; Taubert and Coble, 1977). Gjøsaeter (1978, 1978a) and Gjøsaeter and Blindheim (1978) used the same procedure to age mesopelagic fish species, but the validity of this method has not been confirmed. Growth curves based on this tentative aging technique shows K between 1.81 and 5.62 and L_{∞} from 68 to 77 mm (Fig. 3.5).

Generally, it seems that mesopelagic fish from cold waters are slow growing although growth may be rapid during the first part of life. Warm-water mesopelagic fish seem, however, to have a fast growth, and most of them probably reach maximum size in one year or less. Some species (e.g. *Maurolicus muelleri, Diaphus suborbitale)* seem to have a fast growth until sexual maturity is reached (Gjøsaeter, 1978; Go *et al.*, 1977) and a very slow growth later.

Table 3.4

Parameters of the von Bertalanffy growth equation of various mesopelagic fish

Species	Area	K	L_∞ mm	W_∞ g	t_o	Author
Myctophum affine	Off Japan	0.45	83	-	-	Odate, 1966
Benthosema glaciale	Off Nova Scotia	0.36	68		-	Halliday, 1970
B. glaciale	West Norway, fjords	0.45	75		+0.25	Gjøsaeter, 1973
B. glaciale	West Norway, fjords	0.20	83	8.68	-0.64	Gjøsaeter, 1978
B. glaciale	West Norway, ocean	0.31	75	5.49	0	Gjøsaeter, 1978
B. pterotum	Arabian Sea	1.81	68		-	1/
B. fibulatum	Arabian Sea	5.62	77		-	1/
Diaphus suborbitale	Japan, Suruga Bay	0.11	60	-	2.57	Go *et al.*, 1977
Diaphus dumerili	N. West Africa	3.81	69	-	-	2/
Stenobrachius leucopsarus	Off Oregon	0.34	85	-	-	Smoker and Pearcy, 1970
Lampanyctodes hectoris	South Africa	0.31	100	-	-	Anon, 1974
Notoscopelus kroeyeri	North-east Atlantic	0.89	119	27.56	-0.17	Gjøsaeter, 1978
Maurolicus muelleri	West Norway, fjords	1.05	49	1.45	+0.21	Gjøsaeter, 1978
M. muelleri	West Norway, ocean	0.88	59	2.46	+0.06	Gjøsaeter, 1978

1/ Based on data from Gjøsaeter, 1978a

2/ Based on data from Gjøsaeter and Blindheim, 1978

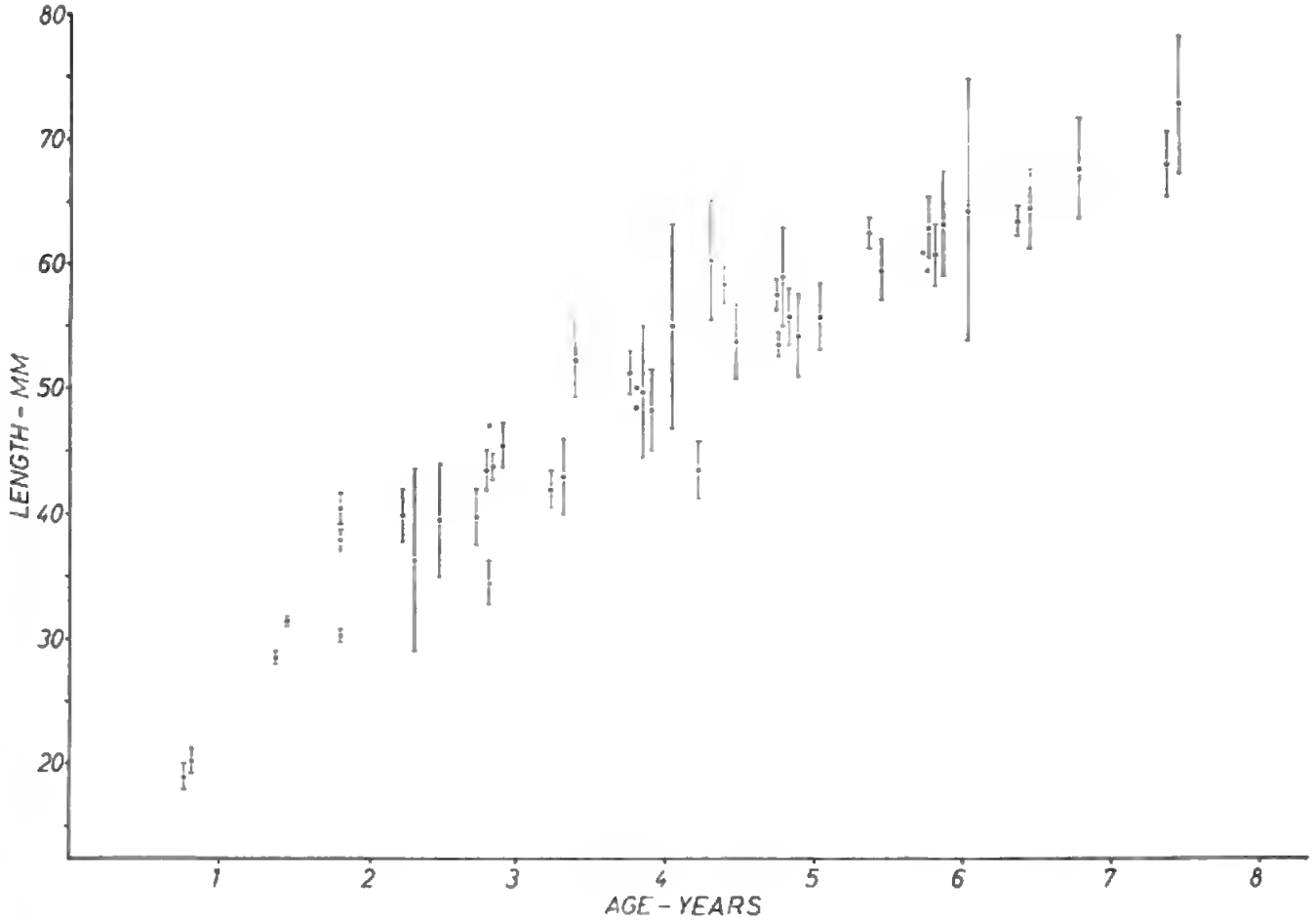

Figure 3.4 Growth of *Benthosema glaciale* from western Norway. The points represent mean length of an age group within a sample and the vertical bars 95% confidence limits. (From Gjøsaeter, 1978)

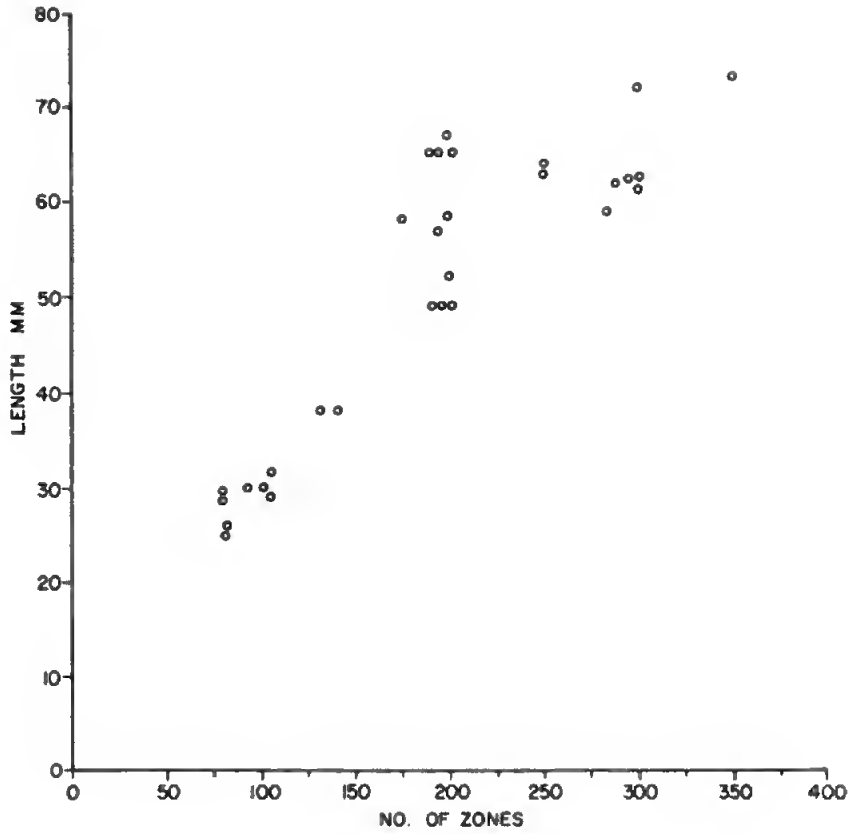

Fig. 3.5 Relationship between length and number of primary zones in the otoliths of *Diaphus dumerili*. (From Gjøsaeter and Blindheim 1973).

Seasonal variation in growth rate has been observed in *Benthosema glaciale* (Gjøsaeter, 1973) and *Diaphus suborbitalis* (Go *et al.*, 1977), the former growing faster in winter and the latter in summer. The differences in growth rate may be related to hydrographic factors.

Most tropical myctophids and smaller gonostomatids seem to have a one-year life cycle (e.g. Clark, 1973, 1974). Based on the tentative ageing carried out by Gjøsaeter and Blindheim (1978) and Gjøsaeter (1978a), *Benthosema pterotum*, *B. fibulatum* and *Diaphus dumerili* all have instantaneous mortality rates of about 5, corresponding to an annual mortality of more than 99%.

Mesopelagic fish from colder waters have a longer life cycle, but few estimates of mortality rates have been made. Gjøsaeter (1973, 1978) estimated the mortality of *Benthosema glaciale*, *Notoscopelus kroeyeri* and *Maurolicus muelleri* to be about 0.7, 0.8 and 1.8 respectively, but due to selectivity of the gears used and other sources of error, these results are only tentative.

Estimates of annual production are also few, and may be strongly biased. For *Notoscopelus kroeyeri*, Gjøsaeter (1978) got 5.9 g/recruit (recruited at one year old). For *Benthosema glaciale* and *Maurolicus muelleri*, both recruited at time t_0, the corresponding values are about 0.4 and 0.2 g respectively (Gjøsaeter, 1978). For tropical species the production could be higher than the standing stock.

3.8 Fecundity

Knowledge of the fecundity of mesopelagic fishes is quite limited. The data accumulated so far for fishes of the Myctophidae and Gonostomatidae are listed in Table 3.5. Among the myctophid fishes, the relation between log F and log L (F = fecundity; L = body length) is similar both intra- and interspecifically. Gjøsaeter (1978) reported that in *Benthosema glaciale*, log F is related to log L by the following equation, suggesting that F is approximately proportional to the body weight:

$$\log F = 3.44 \log L - 3.21 \quad (r^2 = 0.866)$$

In Fig. 3.6, the fecundity of different species of myctophid fishes is plotted against body length. There is a roughly linear relationship between log F and log L, expressed by the following equation;

$$\log F = 3.16 \log L - 5.11$$

Fig. 3.6 shows that the equation is a good fit. At the present stage of study, this empirically derived relationship may be useful in estimating the fecundity of other myctophid species not yet studied, but we do not have enough data to be sure the relationship holds generally.

Among the fishes of the Gonostomatidae, no relationship between F and L such as that observed in the Myctophidae has yet been found, although the data accumulated so far are very few. In three species, *Cyclothone braueri*, *C. microdon* and *Maurolicus muelleri*, fecundity has no relationship to body length (Badcock and Merrett, 1976; Okiyama, 1971; Gjøsaeter 1978), but in *Valenciennellus tripunctulatus*, the number of eggs increases with animal size (Badcock and Merrett, 1976).

Latitudinal variation in fecundity is reported in *Cyclothone braueri* and *C. microdon*, with higher fecundity in a productive area above 30°N latitude in the northeast Atlantic (Badcock and Merrett, 1976).

Table 3.5

Total fecundity counts of some fishes of the families Myctophidae and Gonostomatidae

Species	Number of specimens	$\bar{L}$ (range) in mm	$\bar{F}$ (range)	Sources
Myctophidae				
Benthosema glaciale	6	36.0 (32 - 40)	323 (191 - 467)	Tåning, 1918
B. glaciale	28	57.7 (45 - 75)	781 (162 - 1964)	Gjøsaeter, 1978
Ceratoscopelus maderensis	1	46	2387	Tåning, 1918
C. townsendi	2	77.2 (72.3 - 82.0)	8000 (5150 - 10850)	Bekker & Brodulina, 1968
Diaphus garmani	20	46.3 (41 - 55)	1085 (350 - 1900)	Nakamura, 1970
Diaphus rafinesquei	1	66	2950	Tåning, 1918
Lampanyctus alatus	2	34.5 (30 - 39)	837 (718 - 955)	Tåning, 1919
Lobianchia dofleini	4	34.0 (31 - 40)	388 (330 - 484)	Tåning, 1918
Hygophum benoiti	4	43.8 (42 - 45)	882 (849 - 1273)	Tåning, 1918
Myctophum nitidulum	5	73 (72 - 78)	ca. 8500 (8000 - 9000)	Odate, 1966
M. punctatum	3	54.7 (51 - 61)	852 (792 - 929)	Tåning, 1918
Notolychnus valdiviae	1	22	100	Johnson, 1916
N. valdiviae	1	22	120	Tåning, 1918
Notoscopelus elongatus	1	62	ca. 3600	Tåning, 1918
Gonostomatidae				
Cyclothone braueri	8	26 (24 - 29)	316 (218 - 416)	Badcock & Merrett, 1976
C. microdon	3	47.7 (45 - 49)	2695 (2184 - 3301)	Badcock & Merrett, 1976
Maurolicus muelleri	7	(42.0 - 47.8)	(109 - 331)	Okiyama, 1971
M. muelleri	15	50.8 (47 - 55)	312 (200 - 500)	Gjøsaeter, 1978
Valenciennellus tripunctulatus	?	? (25.5 - 30)	? (200 - 350)	Badcock & Merrett, 1976

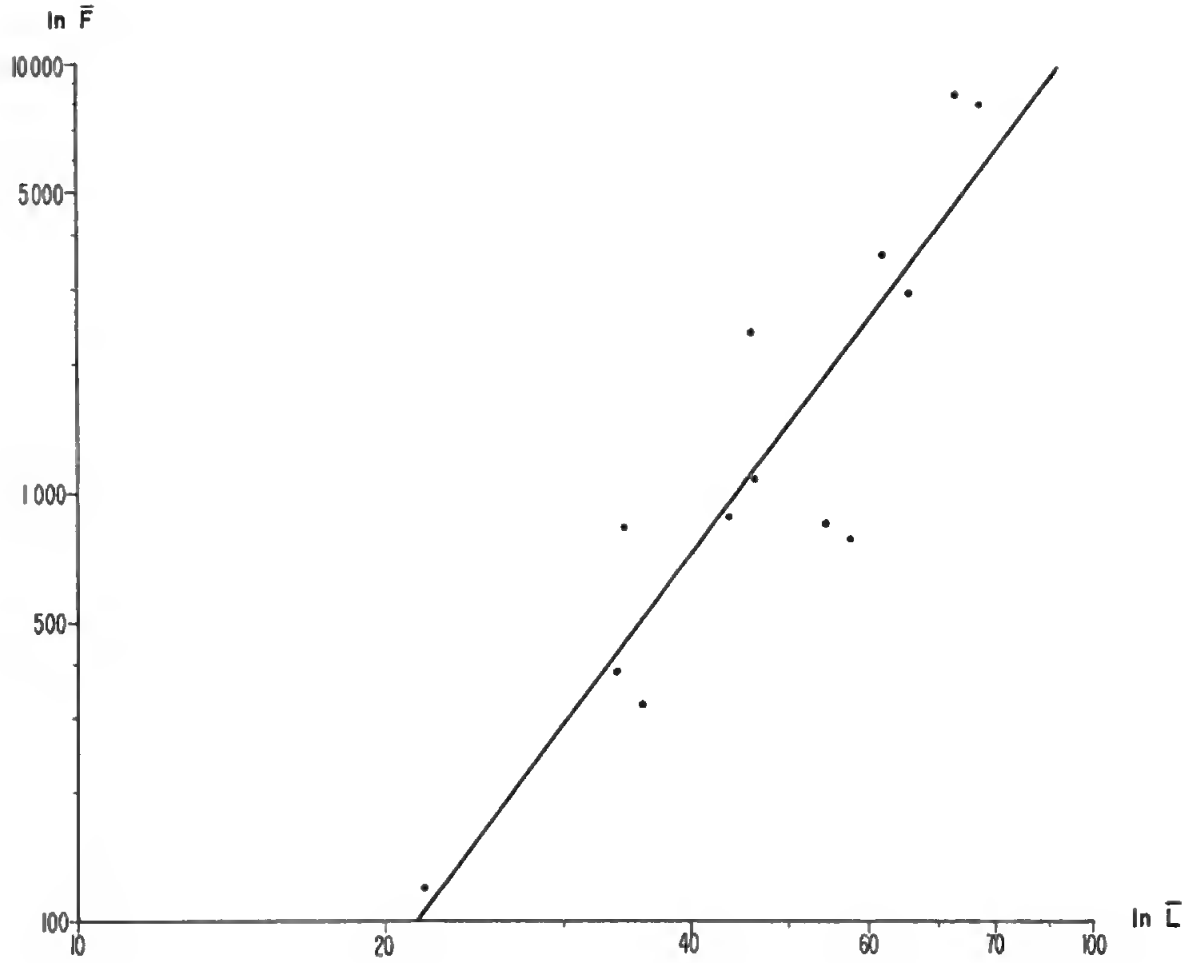

Fig. 3.6 Log-log regression of mean fecundity on mean length for the myctophid species listed in Table 3.5.
The equation is $\ln \bar{F} = -5.11 + 3.16 \ln \bar{L}$

3.9 Spawning seasons

Spawning seasons for myctophid and gonostomatid fishes have been deduced from the maturity stage of the ovary and the seasons in which the larvae occur. The data accumulated so far are listed in Tables 3.6 and 3.7 with their sources. Studies in tropical regions are still few.

Myctophid fishes in temperate and subtropical regions spawn mainly from late winter to summer. Since zooplankton production lags behind the peaks in primary production only slightly, the period of principal spawning for most myctophid species appears to be timed to coincide with the seasonal peak in the production of zooplankton, the main food source (Clarke, 1973). In the subarctic region, *Stenobrachius leucopsarus* is known to spawn in winter (Smoker and Pearcy, 1970). The subantarctic species *Lampanyctodes hectoris* also spawns in winter off New Zealand (Robertson, 1977). Winter spawning in high latitudes seems to be an adaptation to low water temperature, since hatching takes much longer there than in low latitudes. Even in the middle latitudes, the deeper-living species, *Taaningichthys minimum*, *Lampanyctus niger* and *L. nobilis*, tend to have an earlier or longer spawning season. This also might be due to a lower water temperature.

The spawning season of gonostomatid fishes shows a greater variation than that of myctophids, probably reflecting the differences found in their manner of vertical migration, feeding habits, and breeding habits (e.g. sexual dimorphism and sex reversal). For example, the spawning season for species of the genus *Gonostoma*, which are not active diel vertical migrants, differs among species, *G. elongatum* spawning in spring and summer, *G. ebelingi* in early fall, *G. atlanticum* during all seasons in the subtropical central Pacific off Hawaii, and *G. gracile* in fall and winter in the western Pacific (Clarke, 1974; Kawaguchi and Marumo, 1967). Their spawning does not seem to be timed in accordance with the seasonal peak in the abundance of their food. Among species of the genus *Cyclothone*, all of which are non-migrants, a shallow-living species, *C. braueri*, is known to spawn in spring and summer, but the deeper-living species *C. pseudopallida*, *C. pallida*, and *C. atraria* spawn several times a year or during all seasons, or so it would appear from the obscurity of the modes in their size frequency distribution (Badcock and Merrett, 1976; Kawaguchi, unpublished data). On the other hand, the species *Maurolicus muelleri*, *Vinciguerria nimbaria* and *V. poweriae*, which migrate up to the epipelagic zone at night, spawn mainly in spring and summer as observed in many myctophid species (Nishimura, 1959; Clarke, 1974; Gjøsaeter, 1978).

Generally, mesopelagic species in higher latitudes and shallower habitats that are active diel vertical migrants, tend to have a better-defined spawning season than species in lower latitudes and deeper habitats or species of non-migrants. In other words, the migrating or shallow mesopelagic species can sharply perceive and react to the seasonal change in the environmental factors, resulting in a more distinct spawning season.

In regard to the number of spawnings per year, Tåning (1918) could not confirm multiple spawning during his extensive study on the Mediterranean myctophid fishes, but it has been reported for the gonostomatid species *Gonostoma ebelingi* and *Cyclothone pseudopallida* (Clarke, 1974; Badcock and Merrett, 1976). However, at present it is difficult to distinguish multiple spawning from ordinary spawning, since the spawning season is usually long and sometimes ill-defined for many mesopelagic species.

3.10 Life span and age at maturity

Our knowledge of the life span and age of maturity of mesopelagic fishes is confined to a few species of the Myctophidae and Gonostomatidae. In subtropical and tropical waters, the small myctophid fishes *Notolychnus valdiviae*, *Benthosema suborbitale*, *Diaphus schmidti*, *D. anderaeni* and *Lobianchia dofleini* are reported to attain sexual maturity about one year after hatching at a size of 25 to 40 mm SL, and the medium-sized myctophids *Benthosema pterotum*, *B. fibulatum*, *L. dumerili* and *D. suborbitalis* at 50 to 70 mm SL. After breeding, their abundance is known to decrease abruptly, probably owing to death after spawning

Table 3.6

Spawning season of the species of the family Myctophidae
(Sp.= spring; Sum.=summer; F.=fall; W.=winter)

Species	Main spawning season	Areas	Sources
Benthosema glaciale	W. to Sp.	Mediterranean	Tåning, 1918
B. glaciale	Early Sp.	W.N.Atl.(40°-50°N)	Halliday, 1970
B. glaciale	Sum.	Off western Norway	Gjøsaeter, 1978
B. suborbitale	Sp.	Off Hawaii	Clarke, 1973
Bolinichthys longipes	Sp. to Sum.	Off Hawaii	Clarke, 1973
B. supralateralis	Sum. to F.	Off Hawaii	Clarke, 1973
Ceratoscopelus maderensis	Sum.	Mediterranean	Tåning, 1918
C. warmingi	Sp. to Sum.	Off Hawaii	Clarke, 1973
Diaphus anderseni	Sp. to Sum.	Off Hawaii	Clarke, 1973
D. brachycephalus	Sp. to Sum.	Off Hawaii	Clarke, 1973
D. elucens (= *D. perspicillatus*)	Sum.	Off Hawaii	Clarke, 1973
D. fragilis	Sum.	Off Hawaii	Clarke, 1973
D. holti	Sum.	Mediterranean	Tåning, 1918
D. rafinesquei	F. to W.	Mediterranean	Tåning, 1918
D. rolfbolini (= *D. phillipsi*)	Sp. to Sum.	Off Hawaii	Clarke, 1973
D. schmidti	Sp. to Sum.	Off Hawaii	Clarke, 1973
D. suborbitalis	Sp. to Sum.	Suruga Bay, Japan	Go *et al.*, 1977b
Electrona rissoi	Sp. Sum. F.W. (?)	Mediterranean	Tåning, 1918
Hygophum hygomi	F. to W.	Mediterranean	Tåning, 1918
H. proximum	Sp. to early Sum.	Off Hawaii	Clarke, 1973
H. reinhardti	Sp. Sum. F.W. (?)	Off Hawaii	Clarke, 1973
Lampanyctodes hectoris	W. to Sp.	Off New Zealand	Robertson, 1977
Lampanyctus alatus	Sp. Sum. F.W.with a peak in Sp. to Sum.	Mediterranean	Tåning, 1918
L. niger	Late Sum. to W.	Off Hawaii	Clarke, 1973
L. nobilis	Sp. Sum. F.W.(?)	Off Hawaii	Clarke, 1973
L. steinbecki	Sp. to W.	Off Hawaii	Clarke, 1973
Lampadena luminosa	Sp. to Sum.	Off Hawaii	Clarke, 1973
Lobianchia dofleini	W. to Sum.	Mediterranean	Tåning, 1918
L. dofleini	W. to Sp.	w.N.Atl.(32°N,64°W)	Karnella & Gibbs, 1977
L. gemellarii	Sp. to Sum.	Off Hawaii	Clarke, 1973
L. gemellarii	W.	Mediterranean	Tåning, 1918
Myctophum affine (= *M. nitidulum*)	Sp. to Sum.	Off Japan (35°-40°N)	Odate & Ogawa, 1961
M. benoiti (=*Hygophum benoiti*)	Sp. to F.	Mediterranean	Tåning, 1918
M. humboldti (=*Symbolophorus veranyi*)	Sp. to F.	Mediterranean	Tåning, 1918
M. punctatum	W. to Sum. with a peak in Sp.	Mediterranean	Tåning, 1918
M. selenoides (= *M. selenops*)	Sp.	Off Hawaii	Clarke, 1973
Notolychnus valdiviae	Sp. to Sum.with a peak in Sum.	Off Hawaii	Clarke, 1973
Notoscopelus elongatus	W. to Sum.	Mediterranean	Tåning, 1918
Stenobrachius leucopsarus	W.	Off Oregon, USA	Smoker & Pearcy, 1970
S. leucopsarus	W. to Sp.	Off California, USA	Fast, 1960
Taaningichthys minimus	W. (?)	Off Hawaii	Clarke, 1973
Triphoturus nigrescens	Sp. to Sum.	Off Hawaii	Clarke, 1973

Table 3.7

Spawning seasons of some species of the family Gonostomatidae
(Sp.=spring; Sum.=summer; F.=fall; W.=winter)

Species	Main spawning season	Areas	Sources
Cyclothone braueri	Sp. to Sum.	e.N.Atl.(30°N,23°W)	Badcock and Merret, 1976
C. braueri	Sp. to Sum.	Mediterranean	Jespersen & Taning, 1926
C. braueri	Sum.	w. Mediterranean	Goodyear *et al.*,1972
C. pseudopallida	Spawning more than once a year (?)	e.N.Atl.(30°N,23°W)	Badcock & Merrett, 1976
Danaphos oculatus	Sp. Sum. F. W. (?)	Off Hawaii	Clarke, 1974
Gonostoma atlanticum	Sp. Sum. F. W.	Off Hawaii	Clarke, 1974
G. ebelingi	Early Sp. & early F.	Off Hawaii	Clarke, 1974
G. elongatum	Sp. to Sum.	Off Hawaii	Clarke, 1974
G. elongatum	Sp. to Sum.	Subtropical Atl.	Krueger & Bond, 1972
G. gracile	F. to early Sp.	Off Japan	Kawaguchi & Marumo, 1967
Maurolicus muelleri	Sp. to F	Off w. Norway	Wiborg, 1954
M. muelleri	Sp.	Japan Sea	Nishimura, 1959
M. muelleri	W. to Sp.	Off Morocco	Grey, 1964
M. muelleri	Sp. to F. with a peak in Sum.	e.N.Atl.(59°N,19°W)	William & Hart, 1974
M. muelleri	Sp. to Sum.	Off Norway	Gjøsaeter, 1978
M. muelleri	Sp. to Sum.	Off Norway	Bjorke, unpublished
Valenciennellus tripunctulatus	Sp. Sum. F. W.	Off Hawaii	Clarke, 1974
Vinciguerria nimbaria	Sum. to F.	Off Hawaii	Clarke, 1974
V. poweriae	Sp. to Sum.	Off Hawaii	Clarke, 1974

(Clarke, 1973; Karnella and Gibbs, 1977; Gjøsaeter, 1978). The life span of many other medium-sized species in the subtropical and tropical waters remains to be determined. On the basis of growth rates, they probably become sexually mature one year after hatching in highly productive areas, but in areas of low productivity it may take more than two years. The larger myctophid fishes *Lampadena luminosa*, *Bolinichthys supralateralis*, and *Notoscopelus caudispinosus* appear to need more than two years to reach their size maturity, 70-100 mm SL (Clarke, 1973). In temperate or subarctic waters, not only the larger species *Stenobrachius leucopsarus*, but also the medium-sized species *Myctophum affine (= M. nitidulum)* and *Benthosema glaciale*, need two to four years after hatching to attain maturity and their life spans are usually reported to be three to five years (Odate, 1966; Halliday, 1970; Smoker and Pearcy, 1970; Gjøsaeter, 1978).

In the family Gonostomatidae, the smaller species *Valenciennellus tripunctulatus* and *Vinciguerria nimbaria*, are reported to mature within one year after hatching, but the larger fish *Gonostoma elongatum* needs more than two years (Clarke, 1974). Studies on the life span of gonostomatid fishes are very few. Gjøsaeter (1978) recognized three age groups in *Maurolicus muelleri* in Norwegian waters based on an otolith analysis. In the western north Pacific, *Gonostoma gracile* attains sexual maturity as a male one year after hatching, then reverses its sex to female and spawns again at the end of its second year. But cohort size abruptly decreases in the third year, probably due to death just after the second spawning.

3.11 Dwarf males, sex reversal and hermaphroditism

Dwarf males and sex reversal have been known to occur among meso- and bathypelagic species. Marshall (1971) pointed out the ecological significance of these phenomena as an adaptation to a food-poor environment. His hypothesis is supported by the fact that these phenomena are restricted to genera such as *Gonostoma* and *Cyclothone* that do not make a diel vertical migration to feed in the food-rich epipelagic zone (Kawaguchi and Marumo, 1967; Marshall, 1971; Clarke, 1974; Badcock and Merrett, 1976). We cannot find such phenomena in the vertically migrating myctophid and gonostomatid species, which spend the night feeding in the productive epipelagic zone.

Different from dwarf males and sex reversal, hermaphroditism is considered to be an adaptation related to breeding rather than feeding (Marshall, 1971). This phenomenon has been widely reported in the families Paralepididae, Alepisauridae, Evermannelidae, Scopelarchidae and Omosudidae (Mead, 1960; Gibbs, 1960; Mead, Bertelsen and Cohen, 1964; Merrett, Badcock and Herring, 1973).

4. METHODS OF ABUNDANCE ESTIMATION

4.1 Net sampling

Catches made in various types of trawls are the most common source of information on mesopelsgic fish, including abundance. Many types of trawls ranging from small micronekton nets to large commercial trawls have been used, but Isaacs-Kidd midwater trawls (IKMT) and similar gears with mouth areas of 1-10 m^2 have been most common.

When trawls are used there are two main sources of bias to be considered: avoidance (animals sensing the approach of the net and swimming out of its path) and escapement (animals pass through the meshes after entering the net). Both are dependent on size, behaviour, sensing and swimming ability of the fish, and escapement also on body form. Further, they are dependent on the size of the gear, its mesh size, towing speed, etc.

In addition to the bias introduced by avoidance and escapement, the distribution of sampling in relation to the distribution of fish is an important source of variance. Horizontally, the sampling is usually randomly distributed, or distributed according to a predetermined grid of stations, and the fish abundance can, therefore be calculated directly from the mean catch. If, however, the sampling is distributed according to acoustic recordings or other available information on fish distribution, a stratification of the data is necessary to get an unbiased estimate.

Midwater trawl hauls are often oblique and the catch is supposed to represent the mean density in the layer sampled. If the hauls are horizontal, several samples are needed to assess the vertical distribution, or this distribution must be known from other sources.

Micronekton nets

Each kind of net has its own history of modifications to which many workers have contributed. Here, however, we do not intend to review this history. The micronekton nets which have been widely and effectively adopted are the Isaacs-Kidd midwater trawl (IKMT) (Isaacs and Kidd, 1953), the rectangular midwater trawl (RMT) (Clarke, 1969; Baker *et al.*, 1973) and ring trawls, usually 113 or 160 cm in diameter.

All the nets hitherto developed have both merits and demerits related to their structures. IKMT has been widely adopted by many scientists engaged in mesopelagic faunal surveys throughout the world because of its simple structure and ease of handling. It has the advantage over ring trawls of not having large obstacles such as bridles just in front of the mouth, and having an effective depressor which allows high speed towing at a fixed depth. For sampling at fixed depths with IKMT, catch dividing buckets or devices have been developed (Pearcy and Habbard, 1964; Foxton, 1963; Brent, unpubl.), but due to technical difficulties, all the devices are attached to the posterior part of the net instead of the mouth part. These types of codend closing devices are prone to contamination which can be overcome only by using a net equipped with an opening-closing device at the mouth. Isaacs and Brown (1966) described a method for attaching an opening-closing Isaacs-Kidd trawl device at the mouth, but contamination problems still remain (Clarke, 1969).

Rectangular nets have a great advantage over many other types of nets in that the mouth is unobstructed (Tucker, 1951; Davies and Barham, 1969; Clarke, 1969). An opening-closing system at the mouth of the net has been developed for the rectangular net (RMT) by scientists in the U.K. (Clarke, 1969; Baker *et al.*, 1973).

Recently an RMT sampling system with the N.I.O. combination net (RMT_{1+8}) has been developed to collect micronektonic animals over various size ranges (Baker *et al.*, 1973). The system includes an acoustic telemetering system which monitors net depth, relative velocity, total distance travelled, and water temperature, and acoustic opening and closing devices. One problem with the RMT is that the precise volume of water filtered by the nets

cannot be estimated, since the angle of the mouth to the towing direction is variable, depending upon the speed of the net through the water. But Baker *et al.*, (1973) noted that for tows of equal duration "the inverse relationship between net area and distance travelled, combined with the standardization of the fishing procedure and the accurate monitoring of the speed, will tend to minimize the difference between hauls to a level which is probably of little significance compared to other errors inherent in this and any other comparable sampling method (most notably, the irregular distribution of organisms)" and they felt that the "RMT system has now reached a stage where the various nets provide a useful series for reliable routine sampling of a wide size range of organisms in a consistent manner."

Many kinds of ring nets, large conical plankton nets, such as the Indian Ocean Standard Net (Currie, 1962), ORI-net (Omori, 1965; Omori *et al.*, 1965), N_{113} -net (Foxton, 1969) and that adopted by Soviet scientists, etc., have been used to collect micronektonic animals. The common demerit of ring nets is that the bridles probably scare off some active swimmers (Currie, 1962). But its rigid metal ring and bridles assure precise measurement of the volume of water filtered, which recommends ring nets for the sampling of small, inactive swimmers, such as *Cyclothone* and larvae, postlarvae and juveniles of many species.

Sampling limitations of micronekton nets: Because of their small mouth opening, micronekton nets are inadequate for catching larger fishes (more than ca. 5 cm), but they can be caught in commercially-sized trawls (Harrison, 1967). Day-night differences in IKMT catches were studied off southern California to determine biomass, numbers and mean sizes of fishes and decapod crustaceans, resulting in the observation that daytime net avoidance is not a problem with an oblique tow (Atsatt and Seapty, 1974). But the size of the animals studied was usually less than ca. 5 cm. The influence of net speed on the IKMT catch depends not only on species, but also on the size of the animals (Aron and Collard, 1969).

Commercial trawls

Commercial trawls have a large mouth opening (100 - 1 000 m^2), and usually very large meshes (e.g. 20 cm) in the front part, gradually decreasing towards the codend. Due to the large mouth, avoidance is probably negligible. Escapement through the meshes is, however, a serious problem. Usually only the codend has a mesh small enough to retain most size groups of mesopelagic fish. Commercial fish species are led by the large meshes in the front part of the trawl and are finally caught by the finer meshes in the hind part. It is not known, however, to what extent this applies to the smaller mesopelagic fish species. Therefore, it is very difficult to assess the effective mouth opening.

Anon (1976) made two hauls with a 1 360 mesh pelagic trawl and a much smaller trawl, fine-meshed throughout, designed to catch krill. The larger trawl had a mouth opening of about 600 m^2 and the fine-meshed krill trawl about 300 m^2. The codend mesh size was approximately the same in the two nets. The experiments were carried out in an area with very dense concentrations of *Benthosema pterotum*. Although the comparisons were too few to draw final conclusions, they suggest the two trawls catch equal quantities of myctophids. This implies that many of the fish entering the mouth of the larger trawl escaped through the larger meshes toward the front.

Based on these experiments it is supposed that the "effective" mouth area of the 1 360 mesh pelagic trawl is not larger than that of the krill trawl, i.e. about 300 m^2. Later in this paper a 1 600 mesh pelagic trawl which has a larger mouth area, but also larger mesh size will be arbitrarily supposed to have the same effective mouth area.

Experiments carried out by Myrseth (in prep.) in the same area gave slightly different results. He placed bags on various parts of the trawl to catch fish filtered through the meshes. Out of ten experiments, only one gave a large catch of fish in the bags. Salps were, however, often taken in the bags in quantities comparable to those found in the codend. From these experiments it is tentatively concluded that mesopelagic fish are led to some extent by the large meshes in the trawl toward the codend.

Although it is very difficult to draw conclusions on the quantitative characteristics of commercial-sized trawls, there is no doubt that they catch larger mesopelagic fish far better than do micronekton nets, while small species such as *Cyclothone* may be underestimated (Harrison, 1967; Brown and Brooks, 1974). Therefore, to get a complete picture of the mesopelagic fauna it will usually be necessary to use both small and large trawls and even in that case biomass estimates based on trawls will at best be approximations.

Biological factors causing bias in net sampling

For ideal net sampling, we must know the biological or behavioural characteristics of the target species, i.e. swimming behaviour, distributional pattern, development of sensory organs, etc. These factors must be considered in order to decide the size, towing distance, depth, speed, and structure of the net. But unfortunately, our knowledge of micronektonic fishes is inadequate. The difficulty is that we must rely mainly on net sampling to study the biological factors of the fish that bias the net samples. Problems of sample bias have been reviewed by Harrison (1967). The problems include the effect of the distributional pattern and active avoidance of fishes in biasing the catch.

a) Pattern of distribution

Diel vertical migration: Diel vertical migration takes place in many species of mesopelagic fishes, and the pattern is species dependent (see section on diel vertical migration). Generally, the population density is higher at dawn, dusk and during the night than during the day due to the greater vertical extension of distribution during the day. The possibility that gravid females may be unable to take part in diel vertical migration was pointed out for myctophids of the genus *Diaphus* (Nafpaktitis, 1968). This indicates that we must change the towing depth and distance of the net in accordance with time or season of sampling.

Ontogenic vertical migration: Almost all of the mesopelagic species change their vertical distribution range during their life history, with younger individuals usually inhabiting shallower depths (Badcock and Merrett, 1976). Therefore, wide vertical sampling coverage is essential to collect samples representing the true age composition of the population in the sea.

Swarm, shoal, school and patch: Knowledge about schooling or other similar social behaviour, such as size of the school, distance between schools and individual density is necessary to decide sample size, since the net must filter a sufficient volume of water to even out the irregularity of fish distribution (Harrison, 1967). This behaviour has been observed through the window of deep-sea submersibles (Beebe, 1935; Pérès *et al.*, 1957; Barham, 1970, etc.), but present knowledge is still insufficient. Other patterns of irregular distribution due to physical phenomena such as currents, eddies and fronts are also important factors influencing the sample bias.

b) Active responses of the fish to the nets

The problem can be largely divided into two elements: swimming behaviour and sensory ability of the fish.

Swimming behaviour: In general, swimming speed is closely related to body size, shape and feeding behaviour such as filter feeding, luring and darting. A functional morphological approach will contribute greatly to learning about the swimming behaviour of mesopelagic fishes at the present stage, where direct observation by deep-sea submersibles is insufficient and rearing techniques have not yet been established. Active swimmers will not only avoid the net, but also escape from the net mouth.

Vertical orientation: Many individuals of the myctophids *Lampanyctus leucopsarus* and *L. mexicanus*, the bathylagid *Bathylagus stilbius*, the gonostomatid *Cyclothone acclinidens*, the chauliodontids, and the paralepidids have been reported to "hang" in the water at an

acute angle to the horizontal plane (Pérès, 1958; Barham, 1970; see the review by Harrison, 1967). Barham (1970) reported that such inactive, vertically oriented fishes swim rapidly away when stimulated and suggested that fishes actively feeding at night might be nearer their exhaustion point and less capable of making a critical darting action to avoid the net than inactive (resting) fishes during the day. Furthermore, it is possible that vertically oriented fishes of the families Paralepididae and Stomiatidae more easily avoid nets by their upward darting behaviour than those oriented horizontally (Harrison, 1967).

Sensory ability: "The eyes of deep-sea fishes are probably by far the most sensitive in existence" (Walls, 1942, cited by Marshall, 1954:221). This suggests the likelihood of visual net avoidance by mesopelagic fishes, especially in the upper mesopelagic zone (200 - 500 m), during the day. The lateral line organ is also developed in many species and probably plays an important role in the perception of approaching nets. From the viewpoint of functional morphology, a series of counter shading ventral photophores possessed by many mesopelagic species probably indicates their vulnerability to attack from the ventral side. In this context, Harrison (1967) discusses the towing methods of nets - vertical, oblique and horizontal tows.

Much remains to be studied in the future concerning the senory ability to avoid nets. The development of rearing techniques and more direct observations will be essential for these investigations.

4.2 Acoustic surveys

Acoustics have been used intensively in fisheries science and, rather independently, by investigators of the deep scattering layers (DSL). In fish stock assessment, medium frequency echosounders (38 - 50 kHz) and electronic echo integrators have been most commonly used. The general description of the methods and the equipment used are given by Forbes and Nakken (1972), and many of the problems involved are discussed by Margetts (1977). For studies of DSLs low frequency echosounders (e.g. 12 kHz), or explosives and wide frequency range receivers (e.g. 0.5 - 25 kHz) have been commonly used, and the scattering strength as a function of frequency has been recorded. A description of the methods and their application can be found in Farquhar (1971) and Andersen and Zahuranec (1977).

Electronic echo integration at non-resonant frequencies

Generally a hull mounted transducer, an echosounder with a frequency of 38kHz or higher and electronic integrators have been used, but they are now often replaced by digital integrators.

The fundamental principle of the integration method is: when a time varied gain (TVG) compensating for one way geometrical spreading and two-way absorption of sound is applied, and the voltage received from each echo is squared before integration, the output of the echo integrator is linearly related to the biomass of fish per unit area in the sampled part of the water column (see Forbes and Nakken, 1972).

When fish length is much larger than wavelength, the relationship between integrated echo abundance and fish density is well established (Nakken and Olsen, 1977). There is, however, doubt about what happens when the fish length approaches wavelength (approx. 4 cm for 38 kHz).

For mesopelagic fish there is the additional problem that the proportionality coefficient for a given species is seldom known, and therefore it must usually be based on other species. This may introduce bias, although it has been shown that the difference between species decreases as the fish length approaches the wavelength (Nakken and Olsen, 1977).

Another problem with the use of high frequencies is their rather short range. Therefore, the TVG-function usually only covers the upper 500 m, and integration cannot successfully be carried out below that depth.

Resonant frequencies

Scientists studying DSLs mainly use frequencies causing resonance in part of the population studied. Often they use explosives to get a wide range of frequencies, and omnidirectional hydrophones. Usually the working frequencies are between 2 and 15 kHz. The results are usually given as scattering strength of the water column.

One fish giving resonance may contribute as much to the scattering strength as one hundred non-resonant fish. Therefore, estimates based on these methods will in general only include the resonant part of the population. How sharp the resonant peak and therefore the size range giving resonance is, will depend on depth and on several anatomical features of the swimbladder. Abundance estimates based on resonant frequencies can therefore be approximations at best, and as they exclude fish not giving resonance, they will be consistently too low.

For fish lacking a swimbladder, acoustical methods are generally of little use.

4.3 Egg and larva surveys

The errors in stock size estimates based on egg and larva surveys are mainly due to sampling variance and insufficient information on biological factors. In regard to the techniques, Smith and Richardson (1977) published a manual on standard techniques for pelagic egg and larva surveys. Most of their techniques are readily applicable to egg and larva surveys of mesopelagic fishes, although some modification would of course be needed in the depth of sampling.

The main biological factors affecting the estimates are:

1. fecundity
2. sex ratio
3. mortality
4. spawning area
5. spawning season

As discussed in Section 3 on ecology and life history, information on these factors for mesopelagic fish is poor at present, compared with that for commercially important epipelagic species. And there are even more serious problems, such as insufficient knowledge on the identification of eggs and larvae and their vertical distribution patterns.

Identification of most mesopelagic fish eggs has not been established, with the exception of some species such as *Lampanyctodes hectoris*, *Vinciguerria lucetia*, *Maurolicus muelleri* and *Chauliodus barbatus*, etc. (Nishimura, 1957; Ahlstrom and Counts, 1958; Pertseva-Ostroumova, 1973; Robertson, 1977). There have been numerous works on the development of mesopelagic fishes (Myctophidae: Tåning, 1918; Pertseva-Ostroumova, 1964, 1967, 1974; Moser and Ahlstrom, 1970; Shiganova, 1977. Gonostomatidae: Ahlstrom and Counts, 1958; Kawaguchi and Marumo, 1967; Ozawa, 1973, 1976; Okiyama, 1971, etc.). But in spite of these works, the identification of mesopelagic fish larvae is still very difficult, owing mainly to a lack of practical keys to species. It should be stressed here that difficulties in identification are a great obstacle in the way of conducting quantitative egg and larva surveys of mesopelagic fishes.

Concerning the vertical distributional patterns of myctophid eggs, Yefremenko (1977) reported myctophid eggs distributed in the 200 - 500 m layer in the Scotia Sea (near 57°S, 30°W to 60°W), while Robertson (1977) reported the eggs of *Lampanyctodes hectoris* immediately beneath the sea surface. The occurrence of myctophid eggs in the upper mesopelagic zone in the Scotia Sea shows the need for sampling not only in epipelagic zone, but also in the mesopelagic zone below 200 m, during egg surveys of mesopelagic fishes.

Furthermore, there are indications that at metamorphosis some mesopelagic species change their vertical range to depths below the usual daytime habitat of adults (Tåning, 1919; Jespersen and Tåning, 1926; Badcock and Merrett, 1976). These specimens at metamorphosis are essential to larva identification, since they have intermediate morphological characters between postlarvae and adults. This is another reason for sampling in the mesopelagic zone during egg and larva surveys of mesopelagic fish.

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5. NORTHEAST ATLANTIC

The mesopelagic fauna of the Northeast Atlantic Ocean is rather well known, at least from a qualitative point of view. Most studies have, however, been carried out with gears which - at best - should be considered semi-quantitative. Most data from the area are derived from micronekton net collections. Acoustic studies, mainly at resonant frequencies, are also important while data from commercial trawls and from egg and larvae surveys are few. The life history of the few species which are abundant is rather well known.

Abundance

During August 1967, Zahuranec and Pugh (1971) (Table 5.1) occupied four stations in the Norwegian Sea. Biological collections were made with a 6-foot IKMT fully lined with 1/4 inch knotted nylon netting. At their easternmost station (65°N 0°W), 9 tows yielded from 0 to 3 x 10^{-3} fish/m^3. Assuming that the fish were distributed in the upper 500 m, that the trawl had an 85% efficiency (Pearcy and Laurs, 1966), and that the mean weight of the fish was 1 g, a mean biomass of about 2.4g/m^2 can be estimated. 97% of the catches were *Benthosema glaciale*. At the more northern and western stations the catch rates were lower, and about 0.6 and 0.1 g/m^2 were estimated for two stations at above 67°N 4°W amd 68.30°N 8°W respectively. No mesopelagic fish were caught at 69°N 12°W. The size of the *B. glaciale* ranged between about 20 and 65 mm with about 3 equal modes at 30, 41 and 50 mm.

In 1962 seven stations approximately on a line from about 45°N 7°W off the Bay of Biscay to 36°N 14°W off southern Portugal was fished with a 1 600-mesh herring trawl (Krefft, 1974). The average catch was 5.6 fish/min. of trawling. Assuming that the efficiency of the net was similar to that of a 100% efficient trawl with mouth-area 300 m^2 (see Section 4.1), and that the fish were distributed in the upper 1 000 m, this corresponds to a biomass of about 0.2g/m^2. As the size of the fish is not known, the mean weight is arbitrarily set at 1 g. The best catch-rate obtained corresponded to about 1 kg/hour.

Kashkin (1974) occupied one station east of the Azores in June 1967 using a 10-foot IKMT. He got catches about 4 x 10^{-4} to 3 x 10^{-5} fish/m^3 in different depth strata. He reported lengths of the fishes dominating in the different layers ranging from 30 - 40 mm in the most shallow layer to a maximum of 120 mm in one of the deeper layers. He also measured sound scattering at various frequencies and found good agreement between the trawl catches and the acoustic estimates. Based on the data given, a biomass of about 0.5 g/m^2 can be estimated. The data refers, however, only to fish supposed to be important sound scatterers, and therefore underestimates the total biomass.

Badcock and Merrett (1977) occupied three stations at 40°N 53°N and 60°N along the 20 20°W meridian in October 1970, May 1971 and April/May 1971 respectively. They fished horizontal strata between 10 and 1 000 m using an RMT 8. At the northernmost station the biomass was about 1.7 g/m^2 in the upper 1 000 m (assuming a mean weight for *Cyclothone* of 0.2 g and for other fish 1 g). In number, *Cyclothone* made up about 50% of the catches. At 53°N and 40°N the biomass was estimated to 1.5 and 1.1 g/m^2, and the percentage of *Cyclothone* about 60% and 80% in number.

Backus and Craddock (1977) published mean catch in ml/hr for faunal provinces in the Atlantic. Their data are based on nighttime catches in the upper 200 m with a 10-foot IKMT. Assuming that the efficiency of the gear is about 90% (Brooke *et al.*, 1973), that the fish were evenly distributed in the upper 200 m and that there were no fish below this depth during the night, the following results can be derived:

Atlantic Subarctic Region	1.2 g/m^2
Azores - Britain Province	0.1 g/m^2
Mediterranean Outflow Province	0.03 g/m^2

As the figures represent the upper 200 m only, they seriously underestimate the total biomass.

Table 5.1

Abundance estimates derived from trawl surveys in the Northeast Atlantic

Area		Gear	Author	Estimated biomass g/m^2
Norwegian Sea	65°N 0°W	IKMT 6	Zahuranec and Pugh, 1971	2.4
	67°N 4°W	IKMT 6	Zahuranec and Pugh, 1971	0.6
	68.30°N 8°W	IKMT 6	Zahuranec and Pugh, 1971	0.1
	69°N 12°W	IKMT 6	Zahuranec and Pugh, 1971	0.
E. Azores	41°N 14°W	IKMT 10	Kashkin, 1974	0.6
	40°N 20°W	RMT 1+8	Badcock and Merrett, 1977	1.1
	53°N 20°W	RMT 1+8	Badcock and Merrett, 1977	1.5
	60°N 20°W	RMT 1+8	Badcock and Merrett, 1977	1.7
Biscaia - West Portugal		Engel trawl	Krefft, 1974	0.1

Kashkin (1967) has presented data on biomass of mesopelagic fish based on catches obtained in various micronekton nets on a number of cruises. His data are given in g/m^3 and arbitrarily assuming that they represent the mean of the upper 1 000 m they can be converted to g/m^2 surface area. For the Norwegian Sea he got about 0.3 g/m^2. A few hauls west of Iceland yielded about 2 g/m^2. In the best sampled part of the area, west of the British Isles, he got about 0.8 g/m^2, and in the east of the Northwest Atlantic between 0.1 and 0.8 g/m^2.

During 1971 and 1972 Williams and Hart (1974) studied the distribution of fish eggs and larvae at 59°N 19°W. *Maurolicus muelleri* was by far the most important species. Its eggs were abundant from May through August. For both years the mean number of eggs per m^2 surface area was about 100. In 1971 the spawning reached a peak in June when 400 eggs/m^2 were observed. In 1972, 500 eggs/m^2 were taken during the same month. A minimum estimate of the spawning stock can be obtained by considering only the peak of eggs abundance. Assuming a fecundity of 300 (Gjøsaeter, 1978), a sex ratio 1:1 and a mean weight of 1.2 g ($\bar{l}$=45mm), 4 g/m^2 of fish must have contributed to the peak in 1972 and 3 g/m^2 in 1971.

When the incubation time is known, the egg abundance distribution may be integrated to get the total number of eggs spawned during a spawning season, and from this the spawning stock can be estimated. If it is assumed that the eggs of *Maurolicus* hatch after 10 days and that each female spawns once during the spawning season, an estimated spawning stock size of 12 g/m^2 can be derived for each of the two years.

Larvae of various Myctophidae were also caught, but no data suitable for abundance estimation were reported.

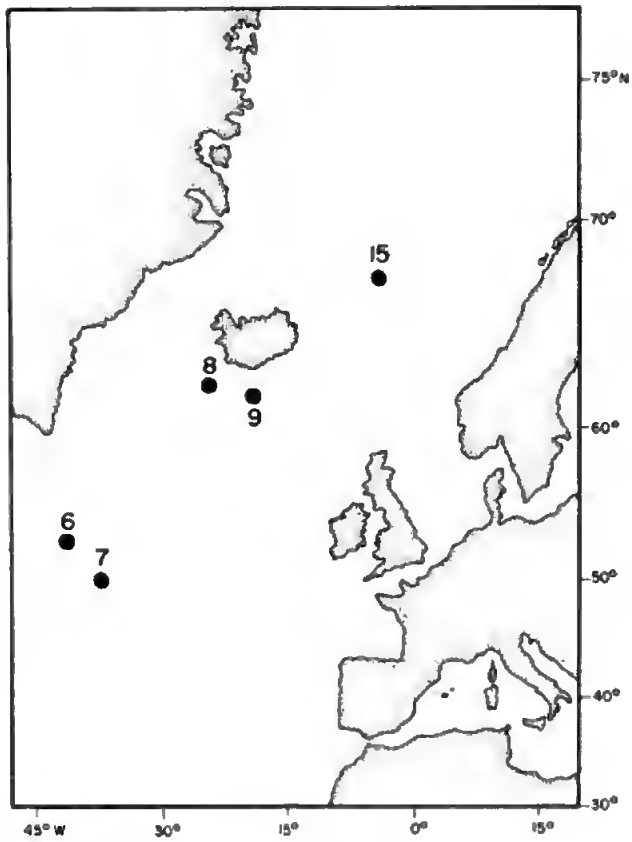

Fig. 5.1 Stations where Chapman *et al.* (1975) made the acoustic measurements referred to in Table 5.1

Gjøsaeter (1978) estimated the abundance of mesopelagic fish off the British Isles and southern Norway using echosoundera and electronic integrators. In Norwegian waters where *Maurolicus muelleri* was the dominant species, stock size estimates within the area covered ranged from 2 000 to 1 600 000 tonnes. (On a large part of the cruises the area of distribution was only partly covered). Generally the biomass was 10 to 35 g/m^2 although the highest average observed over 5 n miles was 160 g/m^2.

West of the British Isles the area from about 51°N was covered during early apring 1972 1973 and 1974. Due to problems with the identification of scatterers and insufficient knowledge about their scattering characteristics only tentative abundance estimates can be derived. If it is assumed that *M. muelleri* was the only mesopelagic fish the biomass in the area covered was about 5, 0.6 and 2 million tonnes in 1972, 1973 and 1974 respectively, or between 6 and 30 g/m^2. An increasing proportion of the two other important species in the area, *Benthosema glaciale* and *Notoscopelus kroeyeri*, will give higher estimates. Assuming *N. kroeyeri* to be the only scatterer will give 13, 2 and 5 million tonnes or more for the three years.

Acoustic studies covering a wide range of frequencies have been reported by Chapman *et al.* (1975), and some of their results from the Northeast Atlantic are summarized in Table 5.2 together with the estimates derived from them. Two stations south of Iceland gave biomass estimates of 1.6 and 0.7 g/m^2 respectively, and two stations in the south-western part of the region gave 1.3 and 1.8 g/m^2. As only fish giving resonance at the frequencies involved will contribute to these values, they will probably be serious underestimates of the true biomass of mesopelagic fish.

Synthesis of abundance estimates

Most of the biomass estimates presented in Table 5.1 are underestimates as the catch rates of micronekton nets were used without considering avoidance, which is probably the most important source of bias (e.g. Scully-Power, 1977). The estimates based on acoustic surveys using resonant frequencies are also underestimates as non-resonant fish will contribute very little to the values obtained. The estimate based on egg samples referred to only one species, and therefore underestimates the total biomass. The data obtained by acoustics at non-resonant frequencies may be over- or underestimates of the true biomass.

It is difficult to find geographical trends in the biomass. There seem, however, to be fairly high concentrations in a zone between western Norway and southern Greenland where about 2 g/m^2 seems to be a conservative estimate. From this zone there seems to be a decrease to the north and to the south. The biomass seems to be very low in the southeastern part of the area where values of about 0.5 g/m^2 were obtained. This is consistent with the observation of Chapman *et al.* (1977) that there was a decrease in scattering strength from the Azores to Gibraltar. The data given by Chapman *et al.*(1975) and Backus and Craddock (1977) indicate an increase in biomass in the western part of the area. Probably the biomass there is higher than 2 g/m^2.

The highest concentrations of mesopelagic fish are, however, found in the neritic areas off southern Norway and to the west of the British Isles. The egg samples from 59°N 19°W indicate that this concentration may extend fairly far offshore. There is little doubt that the mean biomass in these areas is at least of the order of 10 g/m^2. It is not known whether similar concentrations are found near Iceland and southern Greenland.

Table 5.2

Abundance estimates derived from acoustical data presented by Chapman *et al.*, 1975

St. No.	R	Scattering Strength	$\hat{N}/m^2$	$\hat{L}$ mm	$\hat{W}$g	Biomass g/m^2	
6	0.13	-44	1.33	38	0.46	0.6	
7	0.32	-44	0.22	93	8.5	1.9)	
						)	2.3
	0.18	-48	0.28	52	1.5	0.4)	
8	0.24	-44	0.39	70	3.7	1.4)	
						)	1.6
	0.31	-44	0.23	90	7.8	1.8)	
9	0.11	-45	1.47	32	0.25	0.4	
15	no peak						

R is swimbladder radius (cm); $\hat{N}$ is estimated number of fish; $\hat{L}$ and $\hat{W}$ are estimated length (mm) and weight (g) of the resonant fish. For distribution of the stations see Fig. 5.1.

Table 5.3 gives estimates of the stock of mesopelagic fish in the subareas shown in Fig. 5.2. Except for subarea 5 the estimates are based on catches in micronekton nets. For area 5, a mean of the estimates given by Gjøsaeter (1978) is used. For the waters west of the British Isles the lowest estimates were taken, on the supposition that *M. muelleri* was the only sound scatterer.

Table 5.3

Abundance estimates for various parts of the Northeast Atlantic
For areas see Fig. 5.2.

Area No.	Size of Area $m^2 \times 10^{11}$	Biomass g/m^2	Stock tonnes $\times 10^6$
1	7.4	0.1	0.07
2	8.8	0.5	0.44
3	8.6	2.0	1.71
4	12.4	1.5	1.86
5			3.00
6	18.9	1.1	2.08
7	11.2	0.5	0.58
8	25.0	2.0	5.00
	∿ 92		14.74

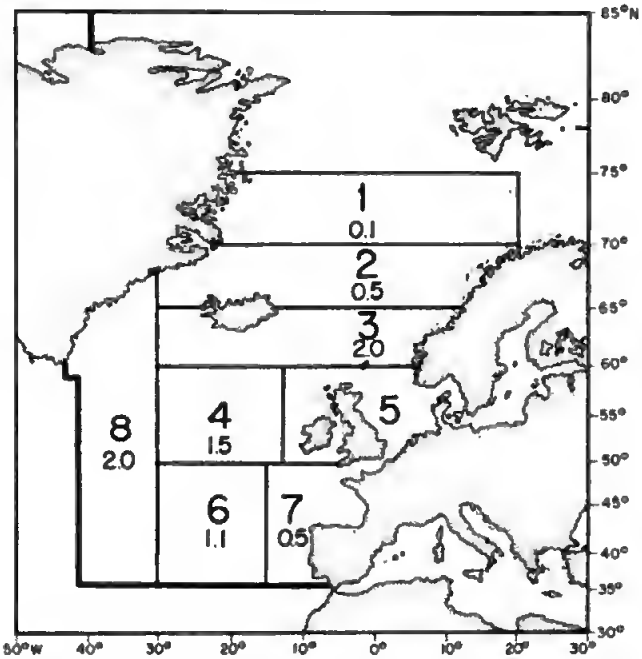

Fig. 5.2 Subareas of the Northeast Atlantic used in the biomass assessment (Table 5.3). The smaller figures indicate mean biomass in g/m^2

Depth distribution

Depth distribution of the DSLs in the Northeast Atlantic was studied by Haigh (1971) using a 10 kHz echosounder. In the Norwegian Sea and Irminger Sea the depth of the only layer found varied from about 250 to 350 m. Between 50° and 60°N the main layer was observed at depths from about 300 to 400 m and in parts of the area an additional layer was observed at about 550 m. Between 35° and 50°N the main layer was usually observed between 350 and 600 m. Additional layers were sometimes observed both above and below these depths. The deepest sometimes extending down to more than 800 m.

Badcock and Merrett (1977) give data based on trawl catches indicating that at 60° the catches were rather evenly distributed between 300 and 1 000 m. At 53°N a maximum was recorded at 500 m depth and at 40°N high catch rates were obtained between 400 and 600 m and at 700 m. At the two northernmost stations good catch rates were obtained in the upper 200 m during the night. At 40°N they found little evidence of vertical migration.

Species composition

Hureau and Monod (1973) give a comprehensive and up-to-date list of mesopelagic fish found in the Northeast Atlantic. The families Myctophidae, Gonostomatidae and Sternoptychidae totally dominate the mesopelagic fauna in the area. For purposes of identification Nafpaktitis *et al.* (1977) should be used for the Myctophidae. For the Gonostomatidae, Grey (1964) should be consulted and for the Sternoptychidae, Baird (1971).

In most of the Northeast Atlantic *Benthosema glaciale* is a dominant species. It is found off south Greenland, Iceland, Spitsbergen and in the western Barents Sea in the north. To the south its distribution extends to the border of the area (Bolin, 1959; Bekker, 1967). It is also abundant in the deep fjords of western Norway (Gjøsaeter, 1973).

Maurolicus muelleri is also very important in the north Atlantic. In neritic areas off southern Norway it is the most important species, and probably it is one of the most abundant species west of the British Isles (Gjøsaeter, 1978). In the north it ranges to the north of Norway and Iceland. In the south it is found beyond the border of the area (Grey, 1964).

Off Great Britain *Notoscopelus kroeyeri* is abundant although the population appears to be expatriated (Gjøsaeter, 1978). Its general range is from about 65°N to about 37°N (Bolin, 1959; Kashkin, 1974).

In the southern part of the area the species *Lobianchia dofleini*, *Lampanyctus pusillus*, *Ceratoscopelus maderensis* and *Argyropelecus olfersi* are also of some importance (Geistdoerfer *et al.*, 1971; Kashkin, 1974; Harrison, 1967; Backus *et al.*, 1977).

Cyclothone seem to be an important component of the oceanic mesopelagic fauna, but due to their very small size (usually less than 30 mm) and their deep distribution they are not of much interest from a practical point of view. The dominant species in the Northeast Atlantic are *C. microdon* and *C. braueri* (Badcock and Merrett, 1977). For a more detailed discussion of the zoogeography of the mesopelagic fish in the Northeast Atlantic, Backus *et al.* (1977) should be consulted.

Life history

Benthosema glaciale is one of the best known mesopelagic fish species as far as life history is concerned (Halliday, 1970; Gjøsaeter, 1973, 1973a, 1978). It seems to have a highly variable growth rate, even within the northern part of the area studied, K from the von Bertalanffy growth curve ranging from 0.19 to 0.46 and L_∞ from 70 to 87 mm. The natural mortality is about 0.7. Sexual maturity is reached after an age of 2 or 3 years and the mean fecundity is about 700 eggs per female. In the southern part of the Northeast Atlantic area the life cycle seems to be shorter and the maximum size smaller.

It feeds partly on copepods and partly on euphausids and belongs therefore partly to the first and partly to the second carnivorous level (Gjøsaeter, 1973a).

Notoscopelus kroeyeri was studied by Gjøsaeter (1978). Its growth can be described by the equation

$$l_t = 119 \text{ mm } (1 - \exp [-0.89(t + 0.17)])$$

and the mortality in the adult population is about 0.8 west of the British Isles. *N kroeyeri* seems to be expatriated, and it is not known where it spawns. The main food is euphausids but some copepods are taken.

Maurolicus muelleri was studied by Gjøsaeter (1978). Its growth can be described by the equation

$$l_t = 59 \text{ mm } (1 - \exp [-0.88 (t + 0.06)])$$

and the mortality rate is about 1.8. Spawning may take place when the fish is one year old, and the number of ripening oocytes per female ranges between 200 and 500. The young fish feed mainly on copepods while copepods and euphausids were about equally important in adult fish.

Aspects of the life history of *Cyclothone* which seem to be important in the oceanic parts of the area have been studied by Badcock and Merrett (1976). Some of their results are presented in Section 7 (Eastern Central Atlantic, where their studies were carried out).

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6. NORTHWEST ATLANTIC

The mesopelagic fauna of the Northwest Atlantic Ocean is rather well known, at least from a qualitative point of view. Most studies have been carried out using micronekton nets, but there are also some data based on direct observations from submersibles and acoustic (resonant frequency) studies. Quantitative estimates based on these methods seem to be divergent, the direct observations from submersibles giving the highest fish densities.

Abundance

The most extensive micronekton net sampling in the Northwest Atlantic was reported by Backus *et al.* (1970) and Jahn and Backus (1976). Jahn and Backus (1976) made 51 collections, partly by a half-lined 10-foot IKMT and partly by fully-lined nets. To make the two sets of collections comparable, those taken by the half-lined nets were multiplied by 1.9. Only nighttime catches in the upper 200 m were used.

Assuming an efficiency of 90% for the gear, the following results are derived:

Slope water	0.2 g/m^2
Gulf Stream	0.1 g/m^2
North Sargasso Sea	0.05 g/m^2

Backus *et al.* (1970), using the same methods, got about 1.7 g/m^2 for the Labrador region. All these figures represent the upper 200 m only, and they therefore seriously underestimated the total biomass, especially in the southern areas, where *Cyclothone* and others which do not migrate to the upper 200 m during the night are important.

Kashkin (1967) has presented data on biomass of mesopelagic fish based on catches obtained in various micronekton nets on a number of cruises. His results are presented in g/m^3 and assuming that the haul represents the mean fish density in the upper 1 000 m they can be converted to g/m^2 surface area. Off southeast Greenland he found about 8 g/m^2 based on 24 hauls. The rest of the area was only poorly sampled, but a much lower biomass (0.3 - 0.7 g/m^2) was indicated.

Acoustical studies covering a wide range of frequencies have been reported by Chapman *et al.* (1975). Some of their results and estimates based on them are presented in Table 6.1. The positions of the stations are shown in Fig. 6.1. A station off southeast Greenland (No. 4) gave 4.7 g/m^2 of a scatterer with length about 10 cm. All other stations except one in northern Baffin Bay (No. 4) where 9 cm scatterers amounted to about 3.6 g/m^2, gave values below 1 g/m^2 and usually below 0.5 g/m^2.

Johnson *et al.* (1956) made a study with a suspended echosounder off the continental slope south of New England (39° 34'N 70° 32'W). The experiment was carried out during the night and the density in the surface layer was too high to be recorded. Between about 70 and 600 m a mean density of 7×10^{-4} fish/m^2 was observed. Assuming that the density in the upper layer is twice that recorded between 70 and 100 m, and that the mean weight of the targets was 1 g, this corresponds to a biomass of about 0.5 g/m^2 surface area.

Backus *et al.* (1968) observed a peculiar sound-scattering-layer at about 40°N 70°W, and observations from a submersible showed that it consisted of schools of *Ceratoscopelus maderensis*. The schools were observed at depths from about 330 m downwards during the day and as shallow as 20 m during the night. This layer was observed in all parts of the slope water, but was irregularly developed. A medium sized school (25 m diameter, 7 m thick) contained about 40 000 fish. The mean size of the fish was about 6 cm corresponding to about 2.4 g. The weight of the fish in one school is therefore about 100 kg. The number of schools was estimated to be about one per 238×10^5 m^3 using echo sounders from surface vessels and one per 7.5×10^5 m^3 using sonarscopes in the submersibles. Taking a mean of these observations and assuming that the schools are distributed in a layer 200 m thick (see Fig. 1 of Backus *et al.*, 1968), the biomass in the area was about 13 g/m^2.

Table 6.1

Abundance estimates derived from acoustic data presented by Chapman *et al.*, (1975)

St.	R	Scattering Strength	$\hat{N}/m^2$	$\hat{L}$	$\hat{W}$	Biomass g/m^2	
1	0.10	-43	2.7	29	0.2	0.5	
2	0.16	-46	0.5	46	0.9	0.5)	
						)	0.8
	0.08	-43	4.2	23	0.1	0.3)	
3	0.13	-47	0.6	38	0.5	0.3	
4	0.36	-40	0.4	104	11.9	4.7	
5	0.13	-47	0.6	38	0.5	0.3)	
						)	0.5
	0.10	-47	1.1	29	0.2	0.2)	
12	0.11	-50	0.4	32	0.3	0.1	
13	0.08	-50	0.8	23	0.1	0.1	
14	0.32	-41	0.4	93	9.1	3.6	

R is swimbladder radius (cm); $\hat{N}$ is estimated number of fish; $\hat{L}$ and $\hat{W}$ are estimated length (mm) and weight (g) of the resonant fish. For distribution of the stations see Fig. 6.1.

Milliman and Manheim (1968) made a dive with the submersible *Alvin* northeast of Cape Hatteras (35° 37'N 74° 49'W) in July 1967. They observed concentrations of myctophid-like fishes exceeding 0.1 per m^3 between 300 and 340 m and more than 0.5 per m^3 at about 570 m. Based on their Fig.2 an abundance of about 100 myctophid-like fish/m^2 surface area can be estimated. The size of the fish was 2 - 6 cm corresponding to a weight about 0.04 - 2.5 g. Assuming a mean weight of 0.6 g ($\bar{l}$ = 4 cm) this corresponds to 60 g/m^2.

Synthesis of abundance estimates

It is difficult to synthesize the estimates available from the Northwest Atlantic as the data are very divergent. It seems that fairly good concentrations are found off south-east Greenland where estimates between about 5 and 8 g/m^2 have been obtained. There are also indications that the slope water off Canada and USA holds a higher biomass than the Gulf Streamwater and the north Sargasso Sea. Although the samples with micronekton nets gave between 0.05 and 0.2 g/m^4 for these areas, acoustic studies indicate that the true values must be considerably higher, at least 0.5 g/m^2. Direct observations indicate values as high as 13 g/m^2 to 60 g/m^2 in the slope waters, but the variation of these concentrations in area and in time is not known.

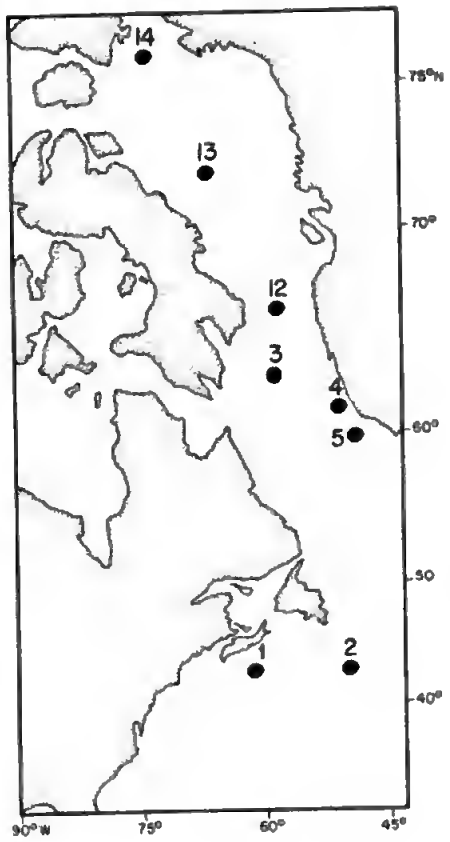

Fig. 6.1 Stations where Chapman *et al.* (1975) made the acoustical measurements referred to in Table 6.1

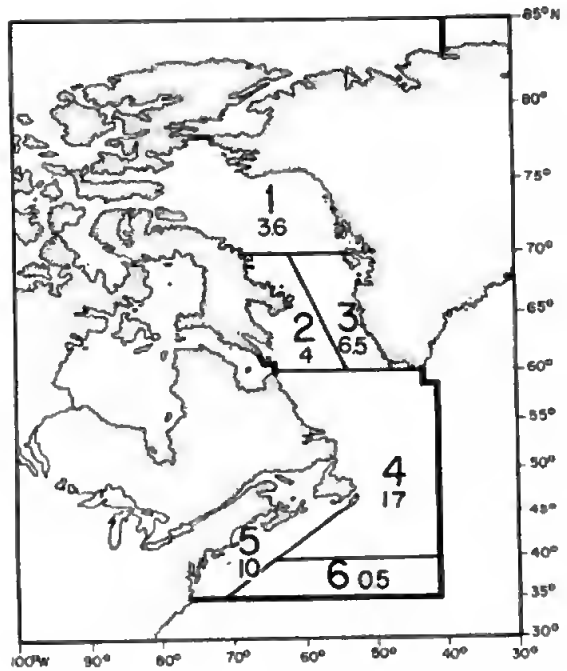

Fig. 6.2 Subareas of the Northwest Atlantic used in the biomass assessment (Table 6.2). The smaller figures indicate mean biomass in g/m^2

With the information available, the figures shown in Table 6.2 can be estimated (for areas used see Fig. 6.2). The estimate for area 4 may be high. The other estimates are probably conservative.

Based on these calculations the stock size in the Northwest Atlantic is about 15 million tonnes, similar to that in the northeast part of the ocean.

Table 6.2

Abundance estimates for various parts of the Northwest Atlantic
For areas see Fig. 6.2.

Area No.	Area $m^2 \times 10^{11}$	Biomass g/m^2	Stock tonnes $\times 10^6$
1	3.0	3.6	1.1
2	1.6	4	0.6
3	1.6	6.5	1.0
4	26.0	1.7	4.4
5	7.2	10	7.2
6	10.0	0.5	0.5
	49		14.8

Depth distribution

The depth distribution of the DSLs in the Northwest Atlantic was studied by Haigh (1971). Using a 10 kHz echo sounder he observed one DSL at about 350 m in the western part of the area and at about 400 - 450 m in the eastern part. Backus *et al.* (1968) observed that the schools of *Ceratoscopelus* found in slope waters were distributed below 330 m during the day and up to 20 m during the night. Off Nova Scotia, Halliday (1970) observed that the most important mesopelagic fish in that area, *Benthosema glaciale*, had a daytime distribution with centre below about 450 m (upper extension 150 m) and a nighttime distribution centred between 45 and 90 m.

Species composition

The families Myctophidae, Gonostomatidae and Sternoptychidae dominate the mesopelagic fauna. For identification, Grey (1964) and Baird (1971) are useful for Gonostomatidae and Sternoptychidae respectively. For Myctophidae, Nafpaktitis *et al.* (1977) give a comprehensive review with keys to genera and species. More details about the zoogeography of the mesopelagic fishes are given by Backus *et al.* (1977).

The relative importance of the different species has been discussed by Backus *et al.* (1970) and Jahn and Backus (1976) and some of their results are presented in Table 6.3. These studies were, however, based on night hauls in the upper 200 m and non-migrants such as *Cyclothone* etc., are therefore excluded.

Table 6.3

Relative importance of the most important mesopelagic fish species in the Northwest Atlantic (data from Backus *et al.* (1970) and Jahn and Backus (1976))

Species	Labrador area	Slope water	Gulf Stream	Northern Sargasso Sea
Benthosema glaciale	1	2		
Ceratoscopelus maderensis	2	3	4	
C. warmingi			2	1
Diogenichthys atlanticus			1	3
Lopidophanes guentheri			3	
Lobiancia dofleini		1		
Notolychnus valdiviae				2
Stomias boa	3			

Life history

Benthosema glaciale has been studied by Halliday (1970) who found that the growth can be described by the equation

$$l_t = 68.28\ (1 - \exp\ [-\ 0.36\ (t + 0.49)])$$

Other aspects of the life history also seem similar in the western and eastern North Atlantic (Gjøsaeter, 1973, 1978).

Lobiancia dofleini from Bermuda waters was studied by Karnella and Gibbs (1977). They found that it reaches a maximum size of about 38 mm, spawns mainly in winter, and has a one-year life cycle.

Notolychnus valdiviae, studied by Gibbs *et al.* (1971), is a very small species. The maximum size in their samples was 22 mm. The species apparently has a one-year life cycle and the spawning seems to increase in intensity from spring to a peak in early summer.

Ceratoscopelus warmingi seem to reach sexual maturity at a length of 40 mm, and the maximum size can be more than 80 mm (Bekker and Borudinula, 1968). In the Bermuda area spawning seems to peak in June or July (Gibbs *et al.*, 1971). In Hawaii waters the species seem to spawn over a long period, but principally during the first half of the year (Clarke, 1973).

7. EASTERN CENTRAL ATLANTIC

From the Eastern Central Atlantic there are data obtained by micronekton nets, commercial trawls, acoustic surveys and larval sampling. For the offshore areas it seems possible, therefore, to obtain a consistent, although conservative, estimate of the biomass. For the coastal waters there are indications of large stocks but more research has to be carried out to obtain a better picture of these concentrations and their variation.

Abundance

Badcock and Merrett (1976) occupied a station at 30°N 23°W during April 1972, fishing horizontal strata between 10 and 1 500 m using an RMT 8. Assuming that the gear has an efficient opening of 8 m^2, two series of 14 dsy hauls and 14 night hauls both indicate a density of between 9 and 10 fish/m^2 (*Macroramphosus scolopax* excluded). Of this, *Cyclothone spp.* made up nearly 70%. If the weight of *Cyclothone* is arbitrarily set at 0.2 g and that of the other mesopelagic fish at 1 g, the biomass is about 4 g/m^2.

Badcock and Merrett (1977) reported similar stations at 18°N 25°W and at 11°N 20°W, but only the water down to 1 000 m was sampled. On the same assumptions as above the following results are obtained.

Position	Fish/m^2	Percent *Cyclothone*	Biomass g/m^2
18°N 25°W	11	65	4.1
11°N 20°W	15	76	6.0

In the period 1966-71 Krefft (1974) made several cruises fishing with a 1 600-mesh herring trawl. Most of the stations in the Central Atlantic fell approximately on a line 35°N 18°W to 0°N 23°W. The mean catch was about 26.5 fish/min. of trawling. Assuming that the efficiency of the net was similar to a 100% efficient trawl with mouth area 300 m^2 (see Section 4.1), that the towing speed was 3.5 knots, that the fish were evenly distributed in the upper 1 000 m and that the mean weight was about 1 g/fish, this corresponds to a biomass of about 0.8 g/m^2.

Blackburn (1977) reported 11 hauls with a micronekton net (type not specified) just beyond the edge of the shelf at about 22°N. He found a fish biomass of about 0.2 g/m^2.

Voss (1969) described the mesopelagic fauna in the Gulf of Guinea. Although no quantitative data are presented, he states that the fauna is very rich, and that IKMT tows gave about ten times higher biomass than comparable tows in the Caribbean Sea.

Kashkin (1967) presented data on the biomass of mesopelagic fish based on catches obtained in various micronekton nets on a variety of cruises. His data is given as g/m^3 and assuming that the hauls represented the mean of the upper 1 000 m they can be converted to g/m^2 surface area. Twentyfive hauls off West Africa north of 10°N gave a mean of 0.6 g/m^2 and 26 hauls south of 10°N and in the Gulf of Guinea gave 4.3 g/m^2.

Backus and Craddock (1977) published the mean catch in ml/hr for faunal provinces in the Atlantic. Their data are based on nighttime catches in the upper 200 m with a 10-foot IKMT. Assuming that the efficiency of the gear was about 90% (Brooke *et al.*, 1973), that the fish were evenly distributed in the upper 200 m, and that there were no fish below this depth at night, the following results can be derived:

North African Subtropical Sea	0.1 g/m^2
Mauritanean Upwelling Region	0.2 g/m^2
Guinean Province	0.2 g/m^2

Gjøsaeter and Blindheim (1978) estimated the abundance of mesopelagic fish off West Africa between 16° and 27°N based on an acoustic survey during November-December 1972. They used a 38 kHz echo sounder and electronic echo integrators. The equipment was calibrated using a 1 600-mesh pelagic trawl. Due to the low efficiency of the trawl, this procedure will usually give underestimates of the true biomass. They also calculated the biomass by using a conversion constant between integrated echo intensity and biomass derived for capelin.

Based on the calibration by trawl they found a biomass of about 6 million tonnes in the area. The highest biomass was observed just off the edge of the continental shelf where a mean biomass of 60 g/m^2 was observed. In offshore waters the mean biomass was 15 g/m^2. Using the density coefficient based on capelin these estimates will be about 3 times higher.

A typical distribution of biomass along a section normal to the shore is shown in Fig. 3.3. From 27°N there was a gradual increase in biomass until Cape Blanc where the highest biomass was observed. Southward the density decreased.

Little trawling was carried out in the mesopelagic fish layer, but in one tow a catch rate of 6 tonnes/hr was obtained. A tow with 0.6 tonnes/hr ranked next. *Diaphus dumerili* was dominant in the catches.

Several studies of fish eggs and larvae have been carried out in the region (Table 7.1). Nellen (1973) studied an area near the Great Meteor Seamount. In oblique tows with a ring trawl down to 200 m he got about 6 larvae/m^2 of each of the families Gonostomatidae and Myctophidae. These made up about 42% of the total larvae caught. Among the Gonostomatidae, *Cyclothone spp.* represented about 73%.

Blackburn and Nellen (1977) studied the nearshore ichthyoplankton at about 22°N. *Maurolicus muelleri* was abundant at the shelf edge (100 eggs/m^2 in part of the area), but the mean in the whole area studied was only 17 eggs and nearly 2 larvae/m^2. Myctophidae represented only one larva/m^2. The mesopelagic fish represented 2.6% of the total fish larvae caught.

Palomera and Rubies (1978), studying a nearshore area between about 23° and 26°N found a mean of about 66 eggs and 20 larvae of *Maurolicus muelleri* per m^2 in stations taken near the edge of the shelf. In the same area they caught 7 myctophid larvae per m^2.

In an area between 10° and 17°N and from the coast to 22°W, Aboussouan and Aldebert (1978) caught a mean of 26 Myctophidae and 12 Gonostomatidae larvae per m^2. The mesopelagic fish made up 74% of all the larvae caught.

As little is known about seasonal variation it is difficult to draw conclusions about adult biomass from larval abundance.

Synthesis of abundance estimates

There seems to be little doubt that the Eastern Central Atlantic is a rich area as far as biomass of mesopelagic fish is concerned. Kashkin (1967) and Backus and Craddock (1977) published results suggesting that the Gulf of Guinea area is among the richest in the Atlantic. It also seems clear that there is a very high biomass in the upwelling area off West Africa. It is not known whether comparable densities may be found in the highly productive parts of the Gulf of Guinea.

The USSR fishing fleet is catching myctophids off West Africa, and according to a questionnaire sent out by FAO, they regard both Myctophidae and Gonostomatidae as potential resources in the Eastern Central Atlantic (W. Fischer, pers. com.). No further information, however, seems to be available about this fishing.

Table 7.1

Number of eggs (E) and larvae (L) of mesopelagic fish per m^2 in the Eastern Central Atlantic. The number of mesopelagic fish larvae as percentage of all the larvae caught is also given

Area	Period	Gonostom. E	Gonostom. L	Myct. L	Mesopel.	Author
29°-31'N 27°-30'W	February 1970		6	6	42%	Nellen 1973
22°N 17-18°W	March-May 1974	17	2	1	2.6%	Blackburn and Nellen 1976
10°-17°N 17-22°W	June-July 1973		12	26	74%	Aboussouan and Aldebert 1978
23°-26°N 14-17°W	April-May 1973	66	20	7	4%	Palomera and Rubies 1978

Table 7.2

Abundance estimates for various parts of the Eastern Central Atlantic (Numbered areas shown in Fig. 7.1)

Area No.	Area size $m^2 \times 10^{11}$	Biomass g/m^2	Stock tonnes $\times 10^6$
1	43	4	17
2	40	6	24
3	7	15	10
4	43	6	26
	133		77

There are, however, few data for estimating absolute abundance. For the northern and western parts of the area the estimates (Table 7.2, Fig. 7.1) are based on micronekton net hauls carried out by Badcock and Merrett (1976, 1977). As there is much evidence that the biomass in the Gulf of Guinea is higher than off the west coast, the biomass there is arbitrarily set at 6 g/m^2. For the Mauritanian upwelling area the most conservative estimate of offshore biomass (15 g/m^2) derived by Gjøsaeter and Blindheim (1978) is used. The very high concentrations of mesopelagic fish observed over the shelf edge are not included in Table 7.2, as they may be temporary phenomena. If they are more stable, and similar concentrations are also found in the upwelling area in the Gulf of Guinea, even the most conservative estimates presented by Gjøsaeter and Blindheim (1978) suggest that these concentrations alone may amount to about 6 million tonnes or more.

The data on eggs and larvae are not used in this assessment but the ratio between number of larvae observed and the estimated biomass does not seem to conflict with what is known about this ratio in other areas.

Depth distribution

Haigh (1971) studied the depth-distribution of the DSLs in the area using a 10 kHz echosounder. In most of the area he found two layers. The most important one had a daytime depth of about 500 - 600 m in the northern and western part, and about 450 m in the more productive upwelling areas. The second layer was observed between about 250 and 400 m.

Badcock (1970) and Badcock and Merrett (1976, 1977) made detailed observations on vertical migration in offshore waters using micronekton nets. They found that during the day the best catches (in number of specimens) were made between 400 and 700 m. The most important Myctophidae were generally caught between 400 and 700 m during the day and from 10 to 100 during the night.

In the Mauritanian upwelling region Kinzer (1977) observed a DSL varying in depth between 80 and 200 m during the day, while *Benthosema glaciale*, which was the dominant species in his RMT 8 catches, was mostly aggregated between 150 and 400 m. Gjøsaeter and Blindheim (1978) using a 38 kHz echo sounder found the main DSLs at a depth between 300 and 500 m during the daytime in the same area. Parts of these layers migrated upwards and made very dense concentrations near the surface during nighttime.

Species composition

The mesopelagic fish fauna of the Eastern Central Atlantic is very rich. For identification of myctophids, Nafpaktitis *et al.* (1977) should be consulted. For stomiatidiform families Grey (1964) and Baird (1971) are useful. A useful checklist is that of Kotthaus (1972).

At a station at 30°N 23°W, Badcock and Merrett (1976) identified 37 families, 66 genera and 98 species. The Myctophidae with 15 genera and 31 species, and the Gonostomatidae with 7 genera and 17 species, were dominant. At 18°N still more species were identified (Badcock and Merrett, 1977).

Table 7.3 shows the 5 species ranking highest in number at stations at 30°N 23°W and off Fuerteventura. Only small species are among the highest ranking, and this may be an effect of the small gears used. Catches with an Engel trawl in the same area were dominated by the myctophids which represented 88% of the fish taken (Harrison, 1967).

Plankton samples from the same general area (Nellen, 1973) gave the following ranking among the mesopelagic fishes:

1. *Cyclothone spp.*
2. *Hygophum spp.*
3. *Vinciguerria spp.*
4. *Lobianchia spp.*

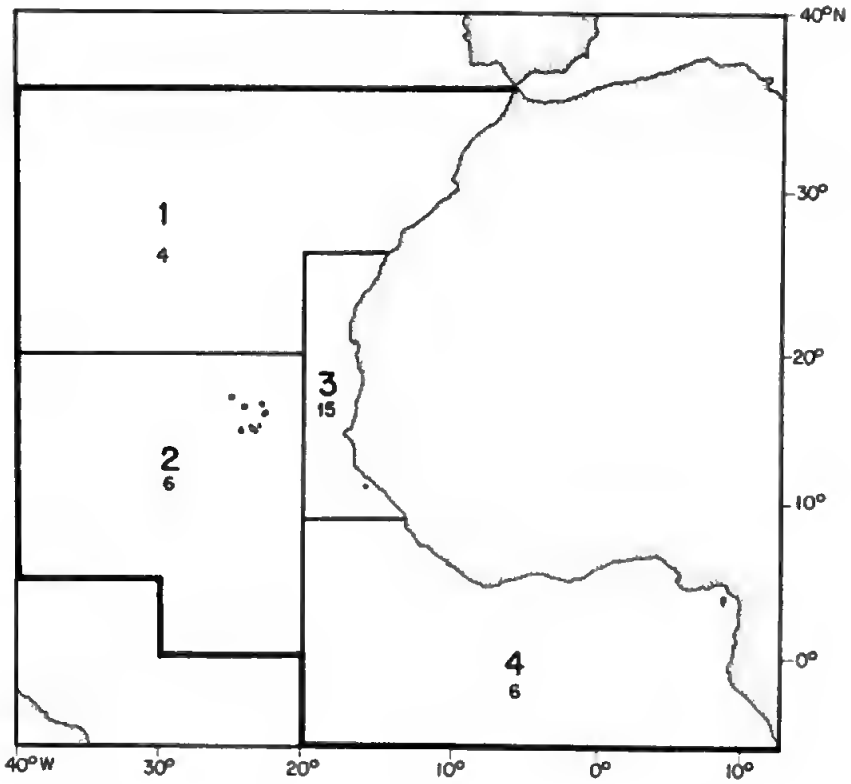

Fig. 7.1 Subareas of the Eastern Central Atlantic used in the biomass assessment (Table 7.2). The smaller figures indicate mean biomass in g/m^2

In nearshore waters between about 23° and 26°N Palomera and Rubies (1976) found larvae of the Gonostomatidae *Maurolicus muelleri* and *Vinciguerria spp.* and the Myctophidae *Ceratoscopelus maderensis, Notoscopelus spp., Diogenichthys atlanticus, Hygophum reinhardti, Lobianchia gemellari, Myctophum punctatum, Lampanychtus sp.* and *Benthosema glaciale* to be abundant. Kinzer (1977) found *Benthosema glaciale* to be far the most abundant species in IKMT catches from this area. Samyshev and Schetinkin (1971) caught *Diaphus dumerili, D. taaningi, Lepidophanes guentheri* and *Maurolicus muelleri* in pelagic trawls. Gjøsaeter and Blindheim found *Diaphus dumerili* to be dominant in catches by large pelagic trawls, followed by *Myctophum punctatum* and *Diaphus taaningi*. According to Backus *et al.* (1977) *Diaphus holti, Lepidophanes guentheri* and *Lampanyctus pusillus* were most abundant in IKMT hauls.

For a more detailed discussion of the zoogeography of the mesopelagic fish in the area, Backus *et al.* (1977) should be consulted.

Table 7.3

Ranking of the most abundant mesopelagic fish species in offshore waters off Northwest Africa

Species	30°N 23°W Badcock and Merrett 1976	Off Fuerteventura Badcock 1970
Cyclothone braueri	1	2
C. microdon	2	
Vinciguerria tripunctulatus	4	
Agyropelecus hemigymnus	3	1
Sternoptyx diaphana		3
Benthosema suborbitale	5	
Lobianchia dofleini		4
Lampanyctus pusillus		5

Life history

The life history of *Cyclothone braueri* was studied by Badcock and Merrett (1976). The species is sexually dimorphic with large females and small males. The size distribution of males was unimodal with a peak at 16 - 18 mm and that of the females was bimodal with peaks at 16 - 18 mm and 23 - 26 mm. Maximum size is about 38 mm. The female matures at a size of about 22 mm and probably spawns only once, at an age of two years. Probably spawning occurs in the spring. The fecundity varies between about 200 - 400 eggs.

Badcock and Merrett (1976) also studied the life history of *Cyclothone microdon*. The males (16-30 mm) are smaller than the females (23-59 mm), and there seem to be at least some cases of sex reversal. The females evidently spawn more than once and the fecundity is about 2 000 - 3 000 eggs.

Diaphus dumerili attains sexual maturity at a length of about 52 mm in the Caribbean, and about 44 mm in the Gulf of Guinea. The maximum size is about 86 mm (Nafpaktitis *et al.*, 1977). Studies of the otolith growth zones suggest that the species may have a one year life cycle (Gjøsaeter and Blindheim, 1978).

For the life history of *Agyropelecus hemigymnus* see Section 11 (Mediterranean).

8. WESTERN CENTRAL ATLANTIC

The northern Sargasso Sea is one of the most intensively studied areas in the world as far as mesopelagic fauna is concerned. For the rest of the Western Central Atlantic the information is more sparse, and based on micronekton net samples and acoustic studies using resonant frequencies, which are both supposed to give underestimates of fish biomass. All data available seem, however, to confirm that the mesopelagic fish biomass in the area is low.

Abundance

The Ocean Acre Programme, designed to study the acoustical and biological characteristics of the DSL in an open ocean area southeast of Bermuda (32°N 64°W), has given a lot of information on the mesopelagic fauna in the northern Sargasso Sea. The principal gear used for biological sampling was a 10-foot IKMT fitted with a four-chambered, discrete-depth cod-end sampler. A 6-foot IKMT and a large Engel trawl were occasionally used (Gibbs *et al.*, 1971; Brown and Brooks, 1974). Acoustical measurements were taken at discrete frequencies ranging from 1.3 to 15.5 kHz (Brooks and Brown, 1977). Brown and Brooks (1974) give a list of works in progress and publications based on Ocean Acre material.

IKMT samples in 50 m depth intervals down to 1 300 m indicated a biomass about 2 g/m^2. Day and night hauls gave similar results (Gibbs *et al.*, 1971; Krueger and Bond, 1972). Only Myctophidae and Gonostomatidae (excluding *Cyclothone*) are included in these values.

The final results of the Engel trawl samples are not published, but it is obvious that the Engel trawl caught larger fish than the IKMT while some abundant small species were virtually absent in the Engel trawl samples (Brown and Brooks, 1974).

Several models have been developed to relate acoustic profiles to fish distribution. The first models showed good agreement in form, but the sound scattering profiles predicted from biological sampling were consistently too low. The reason was probably avoidance of the sampling gears (Scully-Power, 1977). To compensate for this the mean length of the fish caught in the IKMT was adjusted according to a comparison with Engel trawl samples and a better fit was obtained (Brooks and Brown, 1977). (No compensation for avoidance has been applied to the biomass estimate presented in Table 8.3).

Baird *et al.* (1974) studied a DSL in the Cariaco Trench off Venezuela using a modified 6-foot Tucker trawl and acoustic equipment working at 12, 25 and 50 kHz. Based on trawl catches there were about 0.07 fish/m^2. The mean length of *Diaphus taaningi*, which made up about 80% of the catches, was about 41 mm corresponding to 0.6 g. The biomass, therefore, was about 0.05 g/m^2. Based on acoustic data (25 kHz) they estimated a density of about 1.6 fish/m^2 corresponding to nearly 1 g/m^2. Baird and Wilson (1977) also refer to sampling at one station in the Gulf of Mexico and one in the open Caribbean Sea. Based on their data biomass estimates of about 0.02 and 0.04 g/m^2 can be calculated for the two areas. These stations were both placed in areas with very low primary production.

Backus *et al.* (1970) and Backus and Craddock (1977) published the mean catch in ml/hr for faunal provinces in the Atlantic, and their results from the Western Central Atlantic are shown in Table 8.1. The study was carried out and the result converted to g/m^2 as described in Section 5 (Northesst Atlantic). The biomass 0.02 - 0.14 g/m^2 are among the lowest they recorded in the Atlantic Ocean.

Chapman *et al.* (1974) carried out acoustic studies covering a wide range of frequencies, and some of their results from the Western Central Atlantic are summarized in Table 8.2 together with some estimates based on their data. The estimated biomass 0.2 to 0.8 g/m^2 is low, but of the same order as in other parts of the Atlantic Ocean.

Chapman and Marshall (1966), however, obtained densities between about 0.8 and 1.4 g/m^2 of scatterers with swimbladder size 1.8 mm in the northern Sargasso Sea.

Table 8.1

Abundance estimates derived from catches by micronekton nets in the Western Central Atlantic

Author	North Sargasso Sea g/m^2	South Sargasso Sea g/m^2	Gulf of Mexico g/m^2	Caribbean g/m^2	Lesser Antillean Province g/m^2
Backus and Craddock, 1977	0.06	0.02	0.14	0.14	0.08
Baird and Wilson, 1977			0.02	0.04	
Baird *et al.*, 1974				0.05	
Gibbs *et al.*, 1971	0.20				

Table 8.2

Abundance estimates derived from acoustic data presented by Chapman *et al.* (1975)

Area	R	Scattering Strength	$\hat{N}/m^2$	$\hat{L}$	$\hat{W}$	Biomass g/m^2
North Sargasso Sea	.28	-49	0.09	81	5.8	0.5)) 1.1
	.34	-49	0.06	99	10.3	0.6)
South Sargasso Sea	.11	-48	0.7	32	0.25	0.2
Caribbean	.17	-45	0.6	49	1.22	0.8
Lesser Antillean Province	.2	-49	0.2	58	2.21	0.4

R is swimbladder radius (cm), $\hat{N}$ is estimated number of fish, $\hat{L}$ and $\hat{W}$ are estimated length (mm) and weight (g) of the resonant fish

Synthesis of abundance estimates

Although all data available for the Western Central Atlantic are obtained by methods which obviously will underestimate the true biomass, there is little doubt that the mesopelagic fish fauna in the area is poor. This conclusion was reached also by Voss (1966) who stated that the IKMT catches in the Caribbean Sea were only 1/10 of those in the Gulf of Guinea.

Although the biomass probably is lower in the southern than in the northern Sargasso Sea, the biomass derived for the Ocean Acre is used for both (Table 8.3, Fig. 8.1). For the other areas the highest estimates of those presented are used (as all the methods used probably underestimated the true biomass). This gives a total stock size of about 20 million tonnes.

Table 8.3

Abundance estimates for various parts of the Western Central Atlantic

Area	Size of area $m^2 \times 10^{11}$	Biomass g/m^2	Stock tonnes $\times 10^6$
Gulf of Mexico	10	0.14	1.4
Caribbean	16	0.14	2.3
Sargasso Sea	60	0.2	12.1
Lesser Antillean Province	36	0.1	3.6
	- 122		19.4

Depth distribution

The depth distribution of the DSLs in the Sargasso Sea and the Lesser Antillean province was studied by Haigh (1971) using a 10 kHz echo sounder. In the northern Sargasso Sea he found two layers, one extending down from 500 - 550 m. In the southern part of the Sargasso Sea there were layers at 270 - 350 m, 450 - 520 m and 550 - 620 m. In the Lesser Antillean province (*sensu* Backus *et al.*, 1970) two layers at a depth of 300 - 350 m and 500 - 550 m were observed.

Gibbs *et al.*, (1971) and Krueger and Bond (1972) described the depth distribution of the Myctophidae and Gonostomatidae in the Ocean Acre area. During the daytime the best catches of gonostomatids were obtained at depths around 500 m and those of myctophids at 700 m. During the night the best catches were made in the upper 100 m.

In the Cariaco Trench where the deep water is anoxic a DSL was observed at approximately 250 m during daytime (Wilson, 1972).

Species composition

Nafpaktitis *et al.* (1977) reviews all genera and species of the Myctophidae found in the area. A key to the species of myctophids found in the Bermuda Ocean Acre area and some that are expected to be found there is also given by Gibbs *et al.* (1971). For the Gonostomatidae, Grey (1964) and Krueger and Bond (1972) should be consulted, and for Sternoptychidae, Baird (1971).

More than 300 fish species from over 80 families inhabit the Ocean Acre area. The Myctophidae with about 60 species are far more abundant than any other group excluding *Cyclothone*. The Gonostomatidae are second with about 20 species (Gibbs *et al.*, 1971; Krueger and Bond 1972).

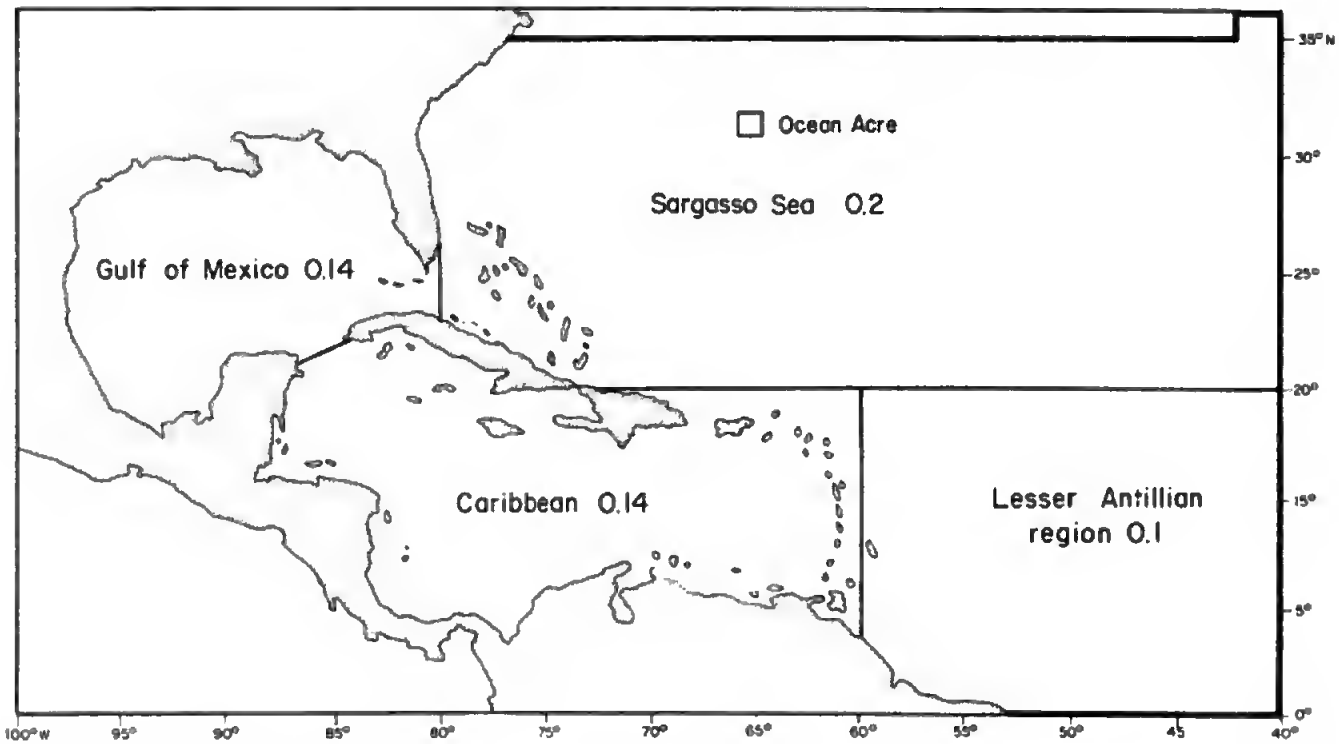

Fig. 8.1 Subareas of the Western Central Atlantic used in the biomass assessment (Table 8.3). The figures indicate mean biomass in g/m^2

According to Gibbs *et al.*, (1971) the following species are numerically dominant among the Myctophidae in the IKMT catches:

Notolychnus valdiviae
Diogenichthys atlanticus
Lampanyctus pusillus
Ceratoscopelus warmingi
Lobianchia dofleini

Among Gonostomatidae *Cyclothone spp.* (mainly *C. braueri*) rank first, followed by:

Vinciguerria attenuata
Bonapartia pedaliota
Pollichthys mauli
Ichthyococcus ovatus

Except for *Cyclothone*, all these rank after the Myctophidae listed (Krueger and Bond, 1972).

The most abundant species according to Backus *et al.* (1970) are listed in Table 8.4. In neritic waters off Venezuela *Diaphus taaningi* seems to be dominant (Baird *et al.*, 1974), while *D. dumerili* is dominant in the Caribbean in general (Nafpaktitis *et al.*, 1977).

Table 8.4

Principal species in shallow (200 m) nighttime collections taken with IKMT (from Backus *et al.*, 1970)

Species	North Sargasso Sea	South Sargasso Sea	Gulf of Mexico	Caribbean	Lesser Antillean Province
Diogenichthys atlanticus	1				
Ceratoscopelus warmingi	2	1		3	
Notolychnus valdiviae	3	3	1	4	2
Pollichthys mauli		4			
Lepidophanes gaussi		2			
Benthosema suborbitale			3		
Diaphus dumerili				1	
Lepidophanes guentheri				2	1
Lampanyctus alatus			2		
L. nobilis					3
L. pusillus	4				

Life history

Diogenichthys atlanticus is a very small species. The maximum size in the Ocean Acre collections was 22 mm. It is presumed that the species has a one-year life cycle and that spawning takes place over a long period with a peak in early spring (Gibbs *et al.*, 1971).

Diaphus taaningi reaches a size of about 50 mm and sexual maturity is attained at a length of 36 - 40 mm. A one-year life cycle, with a few specimens surviving to the second year, is suggested. The spawning season is probably restricted in time, but it is not known exactly when it occurs. The fecundity is about 1 000 eggs per female (Baird *et al.*, 1974).

Vinciguerria attenuata reaches a size of 30 - 48 mm and has a one-year life cycle. Spawning seems to take place during spring (Krueger and Bond, 1972).

For the life history of *Notolychnus valdiviae* and *Ceratoscopelus warmingi*, see Section 6 (northwest Atlantic), and for *Cyclothone braueri* and *Diaphus dumerili* see Section 7 (Eastern Central Atlantic).

9. SOUTHEAST ATLANTIC

Although the southeast Atlantic is one of the few places where commercial fisheries for myctophids have been carried out, little information is available on the mesopelagic fishes of the area. Information on the distribution of species is in preparation, but more surveys are needed to determine the abundance and life histories of the important species.

Abundance

During 1971 Krefft (1974) occupied one series of stations along a line between 0°S 20°W and 35°S 10°W and another between 40°S 20°W and 35°S 17°E. Fishing was carried out with a 1 600-mesh herring trawl, and the mean catch was about 40 fish per minute of trawling. Assuming that the efficiency of the net was similar to that of a 100% effective trawl with mouth area of 300 m^2 (see Section 4.1), that the trawling speed was 3.5 knots, that the mean weight of the fish was 1 g, and that the hauls represent the mean of the upper 1 000 m, the catch rates correspond to a biomass of about 1.2 g/m^2.

Kashkin (1967) presented data on the biomass of mesopelagic fishes based on catches obtained by a variety of micronekton nets during various cruises. His data are reported in g/m^3 and can be converted to g/m^2 by supposing that his hauls represent the mean of the upper 1 000 m. Eighteen hauls near the African coast gave about 3 g/m^2 while 19 hauls in offshore areas gave nearly 1 g/m^2 surface area.

Ahlstrom, Moser and O'Toole (1976) studied the distribution of fish larvae off southwest Africa between 19° and 26°N. All samples were taken nearer to the coast than about 100 n miles. From August 1973 to April 1974, the myctophid larval abundance was higher than 10 larvae/m^2 in about half the area studied. From August 1972 to March 1973 only a small fraction of the area had larval densities above 10/m^2. Myctophid larvae formed nearly 10% of all fish larvae caught, and of these *Lampanyctodes hectoris* formed 85%. About 93% of the larvae of this species were taken during August-November, while 62% of the young larvae (less than 5 mm long) were caught during August, indicating a short, distinct spawning period. The gonostomatid *Maurolicus muelleri* and the myctophids *Symbolophorus boops* and *Diaphus dumerili* were also abundant in the catches (O'Toole, 1974, 1976).

Compared to the larval abundance found in the Arabian Sea (e.g. Nellen, 1973) the values observed off southern Africa are low. They are also lower than the abundance observed off northwest Africa (e.g. Aboussouan and Aldebert, 1978). It is difficult to draw conclusions about the biomass, but as the myctophids off South Africa seem to have a more restricted spawning season than those in the other two areas, it is possible that the stock size relative to that in the other two areas is even smaller than the relative larval abundance. It is, however, not known how large a fraction of the *L. hectoris* stock spawns within the area studied.

Synthesis of abundance estimates

The fisheries carried out suggest that mesopelagic fish may be abundant along the southern African coast, and the larval data published also seem to indicate a higher stock density than that found by Kashkin (1967). His data are nevertheless used for the coastal zone (Table 9.1), as no other estimate is available.

The mean catch rates obtained by Krefft (1974) in the offshore areas were higher than in the other parts of the Atlantic, even though he did not fish in the area occupied by the abundant *Lampanyctodes hectoris*, while those reported by Kashkin (1967) were low compared to his results from other areas. It should, however, be noted that the reliability of Kashkin's results may vary from area to area, as several different cruises are involved. Both studies indicate a mesopelagic fish density of about 1 g/m^2, which is used in Table 9.1. Based on this figure, the biomass of mesopelagic fish in the southeast Atlantic is nearly 20 million tonnes.

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Table 9.1

Abundance estimates for subareas of the southeast Atlantic

Area	Size of area $m^2 \times 10^{11}$	Biomass g/m^2	Stock tonnes $\times 10^6$
Coast of Africa (100 miles offshore)	6	3	2
Offshore	160	1	16
	166		18

Species composition

A discussion of the species composition of the mesopelagic fauna of the area must await the contributions by Hulley (in preparation) and McGinnis (in press).

In coastal waters off South Africa, larval sampling and fishing has shown that *Lampanyctodes hectoris* is the dominant species. Larval sampling has shown that *Maurolicus muelleri* and *Diaphus dumerili* may also be of importance.

Life history

A few life history data for *Lampanyctodes hectoris* have been published (Anon, 1974). According to these the species has a maximum size (L_∞) of about 10 cm and a growth rate of 0.31 (K from von Bertalanffy's growth equation). The fish caught were mostly females, which suggests that there is some connection between the sexual cycle and the pattern of distribution, but so far there is no further information available (Centurier-Harris, 1974).

Life history information about *Maurolicus muelleri* has been given by Okiyama (1971), Gjøsaeter (1978a) and others. Some of this information is presented in Section 5 (Northeast Atlantic).

10. SOUTHWEST ATLANTIC

The information available on the abundance of mesopelagic fish in the Southwest Atlantic is sparse, and particularly so for the highly productive coastal areas. The present data may, however, give a consistent although conservative estimate of the biomass in the oceanic areas, but more work is needed along the shelf. The information on species composition is also sparse, but important studies are in progress on this subject.

Abundance

During the period 1966 - 1971, Krefft (1974) occupied a long series of stations along the line of 40°N latitude and off the coast of South America from 40°S to the equator. Fishing was carried out with a 1 600-mesh herring trawl, and the mean catch per minute of trawling was about 18 fish. Assuming that the efficiency of the net was similar to a 100% efficient net with mouth area 300 m^2 (see Section 4.1), that the speed was 3.5 knots, that the fish were evenly distributed in the upper 1 000 m and that the mean weight was about 1 g/fish, this corresponds to a biomass of about 0.5 g/m^2.

Generally, the best catch rates were about 100 kg per hour of trawling. Just off the edge of the Uruguayan shelf, however, they once got a catch of about 20 tonnes in half an hour. This catch consisted almost exclusively of *Diaphus dumerili* (Krefft, pers. com.).

Kashkin (1967) presented data on the biomass of mesopelagic fish based on catches obtained in various micronekton nets on a variety of cruises. His data are given in g/m^3 and assuming that the hauls represent the mean of the upper 1 000 m, they can be converted to g/m^2 surface area. About 15 hauls were made in the Southwest Atlantic and the mean catch was about 3 g/m^2. Only the area south of about 30°S was sampled and most of the hauls were taken offshore.

Backus and Craddock (1977) published the mean catch in ml/hr in nighttime hauls with a 10-foot IKMT. Their "Amazon Province" approximately corresponds to the Southwest Atlantic north of 10°S and their "South Atlantic Subtropical Sea" partly corresponds to the Southwest Atlantic south of 10°S. In these areas they caught 55 ml/hr and 21 ml/hr respectively. Assuming that the efficiency of the gear was about 90% (Brooke *et al.*, 1973) and that the fish were evenly distributed in the upper 200 m, these catches imply densities of 0.15 and 0.05 g/m^2 for the two areas.

Larval sampling has been carried out off Argentina and eggs and larvae of *Maurolicus muelleri* were caught between 41° and 43°S, but in small quantities only. No other mesopelagic fish larvae were reported (Phonlor, 1973).

Acoustic studies covering a wide range of frequencies have been reported by Chapman *et al.* (1975) and some of their results and the estimates derived from them are shown in Table 10.1. In the region north of about 10°S the resonant biomass was about 1.8 g/m^2. In the South Atlantic Gyre and the subtropical part of the area, about 0.5 g/m^2 was observed. The abundance of resonant scatterers rose again to about 1 g/m^2 in temperate waters, and finally fell to about 0.3 g/m^2 in the Antarctic convergence.

Synthesis of abundance estimates

Although the data presented indicate different levels of abundance, it seems that the biomass of mesopelagic fish is highest in the northern part of the area and in the southern temperate waters. The very high catch rate obtained by Krefft (pers. com.) off Uruguay may indicate that the highly productive coastal waters off South America have large stocks of mesopelagic fish. To confirm this it is, however, necessary to carry out more research there.

Table 10.1

Abundance estimates derived from acoustic data presented by Chapman *et al.* (1975)

Area	R	Scattering Strength	$\hat{N}/m^2$	$\hat{L}$ (mm)	$\hat{W}$ (g)	Biomass g/m^2
North of 10°S	0.18	-44	0.69	52	1.5	1.0
	0.17	-45	0.62	49	1.2	0.8
South Atlantic Gyre	0.19	-50	0.16	55	1.8	0.3
	0.14	-50	0.29	41	0.6	0.2
Subtropical	0.23	-50	0.11	67	3.2	0.4
	0.13	-50	0.33	38	0.5	0.2
Temperate	0.31	-47	0.12	90	7.8	0.9
	0.10	-49	0.71	29	0.2	0.1
	0.24	-47	0.19	70	3.7	0.7
	0.17	-49	0.25	49	1.2	0.3
Antarctic convergence	0.21	-50	0.13	61	2.5	0.3

R is swimbladder radius (cm); $\hat{N}$ is estimated number of fish; $\hat{L}$ and $\hat{W}$ are estimated length (mm) and weight (g) of the resonant fish. For distribution of stations see Fig. 10.1.

To estimate the total stock of mesopelagic fish in the Southwest Atlantic, the region can be divided into three areas, with division lines following 20°S and 40°S latitude. For the southern area, the data presented by Kashkin (1967) are supposed to be the most reliable of those available. For the remaining areas the estimates are based on Chapman *et al.* (1975). It is assumed that not more than half of the mesopelagic fish present are resonant at the frequency bands used. Therefore, the biomass causing resonance has been multiplied by a factor of two. This procedure will certainly give a conservative estimate.

Table 10.2 shows a total estimated biomass of about 40 million tonnes. This excludes stocks which may be found in the highly productive waters just off the shelf.

Depth distribution

No data on the depth distribution of the mesopelagic fish in the area seem to be available at present.

Species composition

A comprehensive checklist of the mesopelagic fish in the area is given by Parin *et al.* (1974). The Myctophidae will also be treated by Hulley (in prep.) and McGinnis (in press).

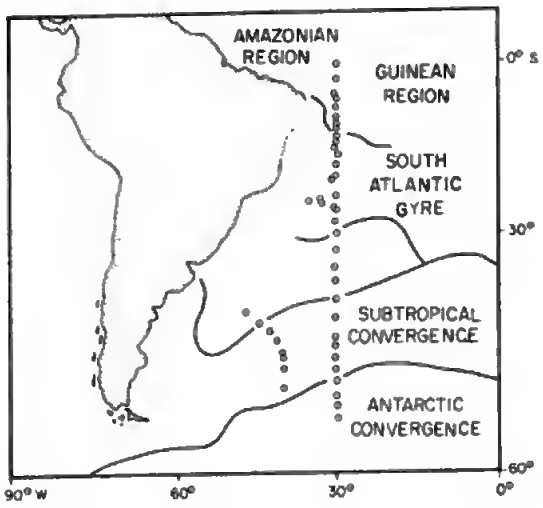

Figure 10.1 Stations where Chapman *et al.* (1975) made the acoustical measurements referred to in Table 10.1. (Redrawn from Chapman *et al.*)

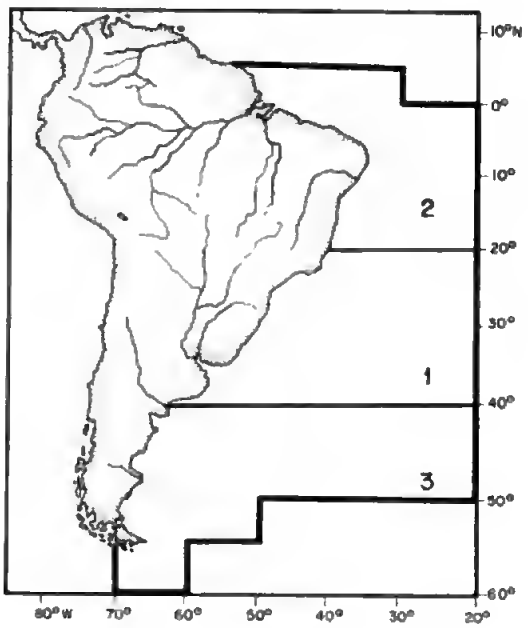

Fig. 10.2 Subareas of the Southwest Atlantic used in the biomass assessment (Table 10.2). The figures indicate the biomass in g/m^2

Table 10.2

Abundance estimates for subareas of the Southwest Atlantic

Area	Size of Area $m^2 \times 10^{11}$	Biomass g/m^2	Stock Tonnes $\times 10^6$
North of 20°S	60	2	18
20°S - 40°S	60	1	6
South of 40°S	50	3	15
	180		39

Parin *et al.* (1974) found *Cyclothone* spp. (mostly *C. microdon*) to be the most abundant fish in the area followed by *Bathylagus antarcticus, Gymnoscopelus braueri, Diaphus theta* and *Vinciguerria nimbaria. Diaphus dumerili* which Krefft (pers. com.) found to be densely concentrated off Uruguay was caught only in small numbers by Parin *et al.* (1974).

A more detailed description of the species composition and distribution of the species within the area must await the contributions from Hulley (in prep.) and McGinnis (in press).

Life history

The life history of *Cyclothone microdon* has been described by Badcock and Merrett (1976) and some of their results are presented in Section 7 (Eastern Central Atlantic).

A few life history data on *Diaphus dumerili* were given by Nsfpaktitis (1968) and by Gjøsaeter and Blindheim (1978). These are summarized in Section 8 (Western Central Atlantic).

For the other important species found in the area, life history information is very sparse.

11. MEDITERRANEAN SEA

Studies of mesopelagic fish have long a tradition in the Mediterranean. Important contributions were presented as early as 1918 (Tåning, 1918). The life history of the important species is, therefore, well known compared to what is known about species in most other areas. Quantitative data are, however, still few, and they all refer to oceanic areas.

Abundance

In 1970 sampling was conducted with a 10-foot IKMT fully lined with ¼-inch bar mesh. The results have been presented as specimens/hr (Goodyear *et al.*, 1972) and in Table 11.1 they are converted to g/m^2 by supposing that the filtering efficiency was 90% (Brooke *et al.*, 1974), that there were no fish below 1 000 m, and that the towing speed was 3 knots (not stated). The mean length of the fish seems to have been about 20 mm (Appendix tables to Goodyear *et al.*, 1972), probably corresponding to a weight of about 0.1 g. In the central area (station 5) there is not sufficient data to estimate the biomass, but apparently it is similar to, or slightly lower than that at station 2.

Backus and Craddock (1977) published the mean catch in ml/hr for the western and eastern Mediterranean Sea. Their data are based on nighttime hauls in the upper 200 m with a 10-foot IKMT. Assuming that the efficiency of the gear was about 90% (Brooke *et al.*, 1973), that the fish were evenly distributed in the upper 200 m and that there were no fish below this depth during the night, the following results are derived:

Western Mediterranean Sea	0.5
Eastern Mediterranean Sea	0.03

As *Cyclothone* spp., which by far outnumbers all other species in the area (Goodyear *et al.*, 1972), never enters the upper 200 m these figures seriously underestimate the true biomass.

Table 11.1

Fish abundance at the stations occupied by Goodyear *et al.* (1972). (See Fig. 11.1)

Station	Fish/m^2 surface	
	Day	Night
1	5.5	3.3
2	9.1	5.5
3	3.3	2.7
4	slightly lower than station 3	
5	0.7	3.5

Acoustic studies covering a wide range of frequencies have been reported by Chapman *et al.* (1975) and some of their results from the Mediterranean Sea are summarized in Table 11.2 along with the estimates derived from them. Both stations show a fairly large biomass and they indicate that size groups not taken by IKMT may be of importance in the area.

Table 11.2

Abundance estimates derived from acoustic data presented by Chapman *et al.* (1975)

Area	R	Scattering Strength	$\hat{N}/m^2$	$\hat{L}$	$\hat{W}$	Biomass g/m^2 Each size group	Total
Ligurian Sea	0.37	45	0.13	107	13.2	1.7)	
	0.23	49	0.13	67	3.2	0.4)	2.4
	0.12	47	0.78	35	0.3	0.3)	
Tyrrhenian Sea	0.35	46	0.12	102	11.2	1.3)	
	0.25	49	0.11	73	4.2	0.5)	2.2
	0.16	48	0.35	46	1.0	0.4)	

R is radius of swimbladder (cm); $\hat{N}$ is estimated number of fish; $\hat{L}$ and $\hat{W}$ are length (mm) and weight (g) of the resonant fish

Synthesis of abundance estimates

The information available is sparse, but it seems clear that the biomass of mesopelagic fish in the Mediterranean Sea is low, and lower in the eastern than in the western part.

The fish densities used for the western part of the Mediterranean Sea and the Tyrrhenian Sea (Table 11.3, Fig. 11.1) are those based on Chapman *et al.* (1975), raised slightly to compensate in part for non-resonant fish. These data, derived from acoustic work, are chosen as they show that size groups not commonly caught by IKMT are of importance. For the other areas the estimates are based on Goodyear *et al.* (1972), as no other data are available.

Depth distribution

Goodyear *et al.* (1972) give data on depth distribution of all the important species of mesopelagic fish caught by IKMT. During the daytime they caught mesopelagic fishes between 100 and 1 000 m with peak concentrations at various levels from 375 to 1 000 m. During the night peaks were observed at 0-100m and 400 - 800 m.

Species composition

An up-to-date list of mesopelagic fish found in the Mediterranean is given by Hureau and Monod (1973). For identification of specimens the works listed for the Northeast Atlantic should be consulted.

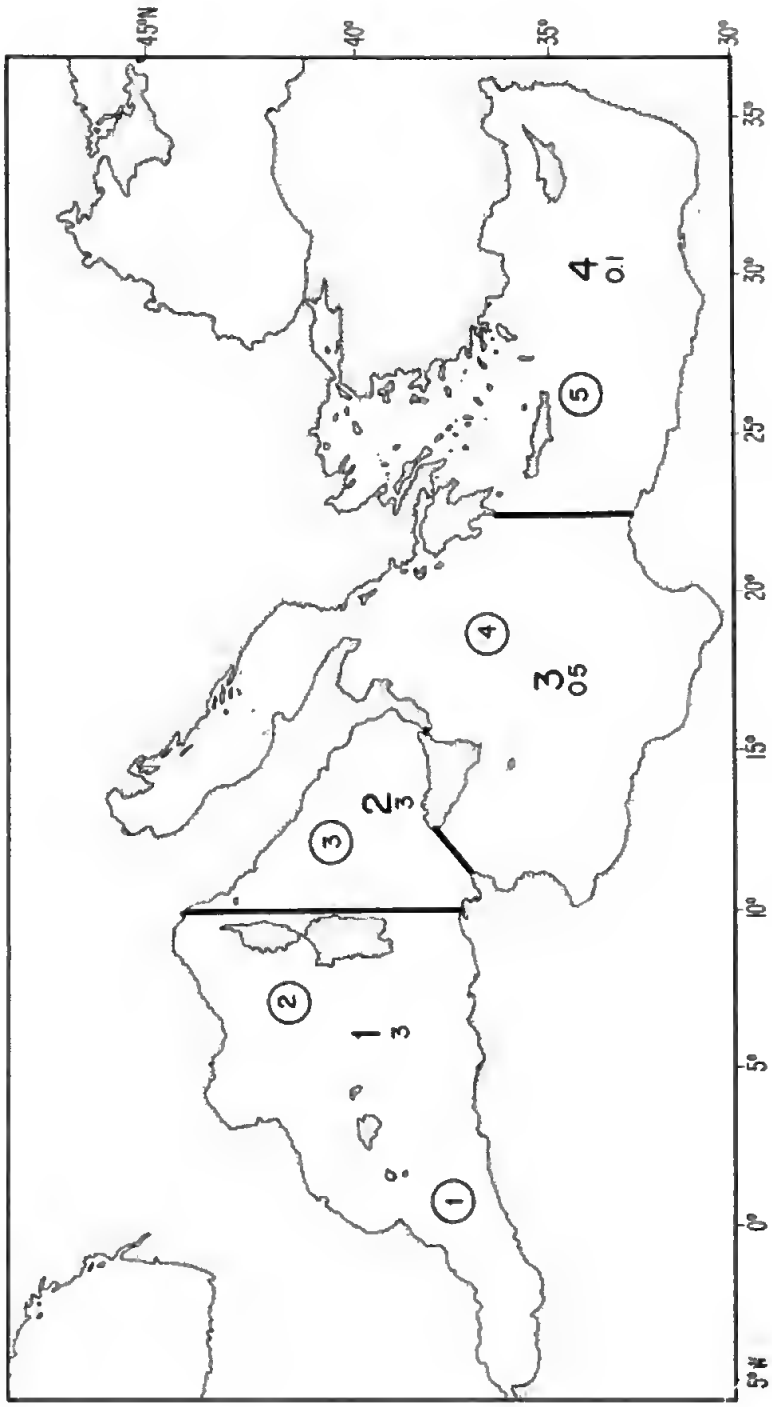

Figure 11.1 Subareas of the Mediterranean used in the biomass assessment (Table 11.3). The stations referred to in Table 11.1 is also shown. The small figures indicate the biomass in g/m^2

Table 11.3

Abundance estimates for various parts of the Mediterranean Sea
For areas see Fig. 11.1

Area	Size of area $m^2 \times 10^{11}$	Biomass g/m^2	Standing stock tonnes $\times 10^6$
1	4.6	3	1.4
2	2.4	3	0.7
3	6.8	0.5	0.3
4	4.6	0.1	0.05
	18.4		2.45

Table 11.4

Rank of catch rates in IKMT in the Mediterranean Sea
Based on data from Goodyear *et al.* (1972)

Station Area	Off S.E. Spain	W. of Corsica	Tyrrhenian Sea	Ionian Sea	S. of Crete
Cyclothone braueri	1	1	1	1	1
C. pygmea	2	2	3	2	4
Benthosema glaciale	3	3			
Ceratoscopelus maderensis	4	4	2		3
Lampanyctus pusillus		4	4		
Hygophum benoiti				3	
Lobianchia dofleini				4	
Gonichthys cocco					2

Goodyear *et al.* (1972) found that *Cyclothone braueri* gave the highest catch rates in all areas of the Mediterranean (Table 11.4). Among the most important myctophids were *Benthosema glaciale, Ceratoscopelus maderensis* and *Gonichthys cocco*.

Aboussouan (1971) collected fishes off the Provence coast using an IKMT. The Sternoptychidae (*Argyropelecus hemigymnus*) made up 16%, Gonostomatidae (mostly *Cyclothone braueri*) 27%, and Myctophidae (most *Benthosema glaciale* and *Diaphus raphinesqui*) only 8% of the catches.

Dekhnik and Sinyukova (1966), studying fish larvae, found that the Gonostomatidae (*Cyclothone* and *Vinciguerria*) dominated, followed by the Myctophidae of which *Diaphus holti* and *Ceratoscopelus maderensis* made up the densest concentrations.

Life history

The life histories of important mesopelagic fish species from the Mediterranean have been studied by Taning (1918), Jespersen and Tåning (1926) and Goodyear *et al.* (1972). Most of the following account is based on Goodyear *et al.* (1972).

Cyclothone pygmea are much smaller than fish of the same species in the North Atlantic. The maximum size seems to be about 41 mm and sexual maturation occurs at a length between 30 and 35 mm in both males and females. Spawning probably peaks in late spring and summer, after which the adults die.

Ceratoscopelus maderensis reach a size of about 70 mm. All specimens larger than 38 mm seem to be mature, and spawning apparently occurs in spring and summer. Probably the species has a one-year cycle and the older fish die after spawning.

Hygophum benoiti is a small species reaching a maximum size of about 45 mm. Sexual maturity is reached at a length of about 30 mm and a one-year life cycle is suggested. Spawning apparently peaks in spring and summer.

Argyropelecus hemigymnus seem to reach a size of 20-24 mm, the males being slightly smaller than the females. There seems to be a restricted breeding season, and most of the adults apparently die after spawning.

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12. WESTERN INDIAN OCEAN

The Arabian Sea has been fairly intensively studied as far as mesopelagic fish are concerned. Acoustic records, egg and larva counts and catch data from micronekton nets and commercial trawls are all available. For the southern Indian Ocean much less information is available and most data are from micronekton nets, although acoustic equipment with echo integration and commercial trawls have been used off Mozambique and the Seychelles.

Abundance

During the Indian Ocean Expedition, R/V ANTON BRUUN collected mesopelagic fishes between 10°N and 45°S along 60°E and between 18°N and 40°S along 65°E. The gear used was a 10-foot IKMT. The two most abundant families caught were the Myctophidae (Nafpaktitis and Nafpaktitis, 1969; Nafpaktitis 1978) and Gonostomatidae (Craddock and Haedrich, 1973). Generally the catch rates were low. Assuming that about 4×10^4 m²/hr of water was filtered and that the efficiency of the gear was 90% (Brooke *et al.*, 1973), only a few stations yielded more than 1 fish/m² surface area. Only two stations in the Arabian Sea (16° 05' and 17° 46'N 65°E) gave catch rates of about 2.5 and 3.5 fish/m², corresponding to between 1.5 and 2 g/m². Three species, *Hygophum proximum*, *Bolinichthys longipes* and *Diaphus thiollieri*, were dominant at these stations.

During autumn 1964, R/V TE VEGA made a cruise from Mombasa to Sri Lanka (Bradbury *et al.*, 1974). Mesopelagic fish was caught with a 10x10 ft Tucker trawl. The towing speed was 1 to 1.5 knots and catches were generally low, the best one yielding about 220 fish of which more than half were *Cyclothone*. This may correspond to about 1 - 2 g/m². Other stations indicated a density of about 0.5 g/m² or lower. It is not possible to assess any trend in the abundance along the cruise track.

During 1975 and 1976, R/V Dr. FRIDTJOF NANSEN worked in the Arabian Sea making five surveys between Mogadishu and the India-Pakistan border (Anon, 1978). On these surveys the mesopelagic fish were studied using 38 kHz echo sounders with electronic integrators and commercial-sized pelagic trawls (Gjøsaeter, 1978a). The abundance estimates based from echo integration are shown in Table 12.1. The areas used are shown in Fig. 12.1. In terms of biomass per unit surface area, the mean densities varied from about 80 - 200 g/m² in the Gulf of Oman to about 20 g/m² off Somalia (Fig. 12.1). The highest concentrations were usually observed just off the shelf break. Trawling confirmed that the densities of fish were high in some areas and 26 stations gave catch rates higher than 400 kg/hr of mesopelagic fish (Table 12.2 and Fig. 12.2). The highest catch rate obtained was 20 tonnes/hr. Catches with a fine-meshed krill trawl indicated that the best concentrations could reach 8 fish/m³.

During January-June 1977 a similar study was carried out off the coast of Pakistan (Anon, 1978a; Myrseth, in prep.). The area shown in Fig. 12.3 was covered five times, and the abundance estimates ranged from about 3 to 13 million tonnes. Catch rates of 2 - 5 tonnes/hr were obtained in pelagic trawl hauls.

During 1977/78 the Gulfs Regional Fishery Survey and Development Project (FAO) surveyed the Gulf of Oman using acoustic equipment (Anon 1978a). During November 1977 and May 1978 they found 4.60 and 2.75 million tonnes of myctophids. Concentrations between 50 and 500 g/m² were commonly found, and in some places the fish density was higher than 500 g/m². The concentrations were highest along the edge of the continental shelf. They also observed that the stock size was slightly higher in the southern than in the northern half of the Gulf.

During a cruise in September 1978, they again recorded dense concentrations (50-500 g/m²) along the edge of the continental shelf in the southern part of the Gulf of Oman, while concentrations were very low in the central and northern parts (Lamboeuf and Simmonds, unpublished report to FAO).

During the period August 1977 to June 1978, R/V Dr. FRIDTJOF NANSEN worked off Mozambique. The area from the coast to a maximum of about 100 n miles off the slope and from 10° to 27°S were covered four times. The data are still being processed, but preliminary calculations

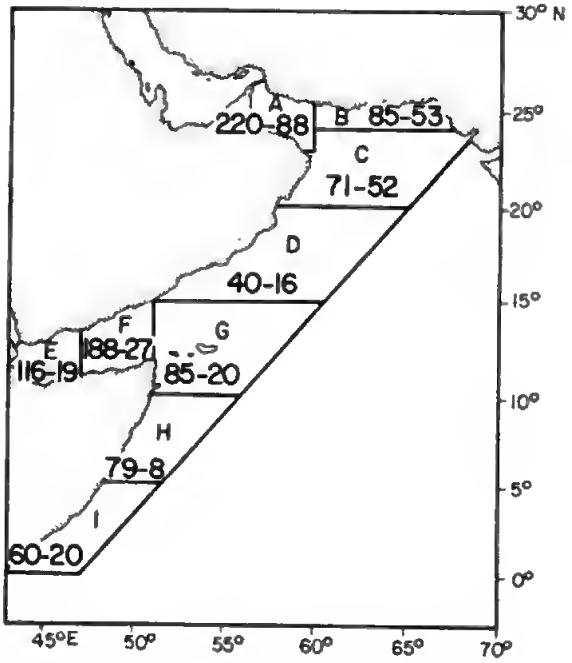

Fig. 12.1 Areas studied by R/V Dr. FRIDTJOF NANSEN January 1975 - November 1976. The figures indicate the highest and the lowest mean biomass (g/m^2) observed in the subareas

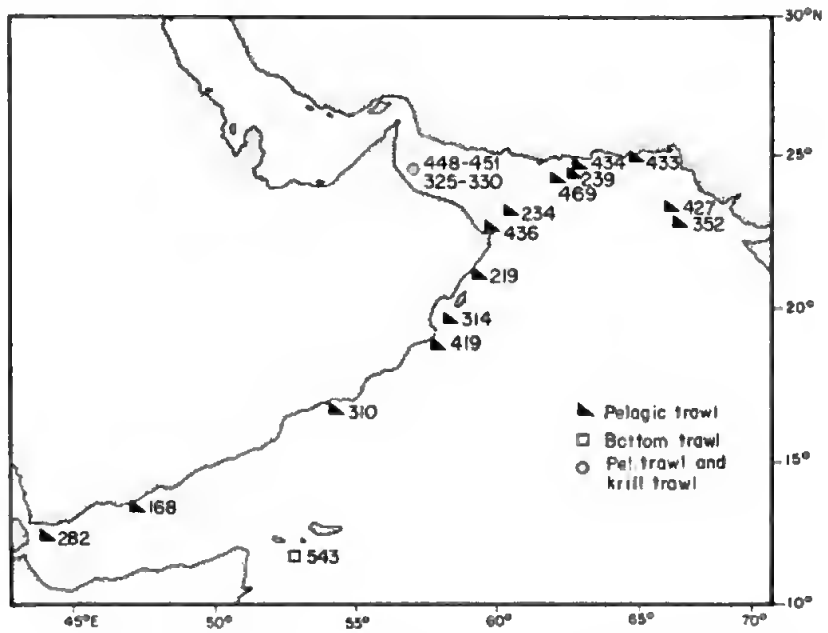

Fig. 12.2 Trawl stations taken by R/V Dr. FRIDTJOF NANSEN giving more than 400 kg mesopelagic fish/hr of trawling

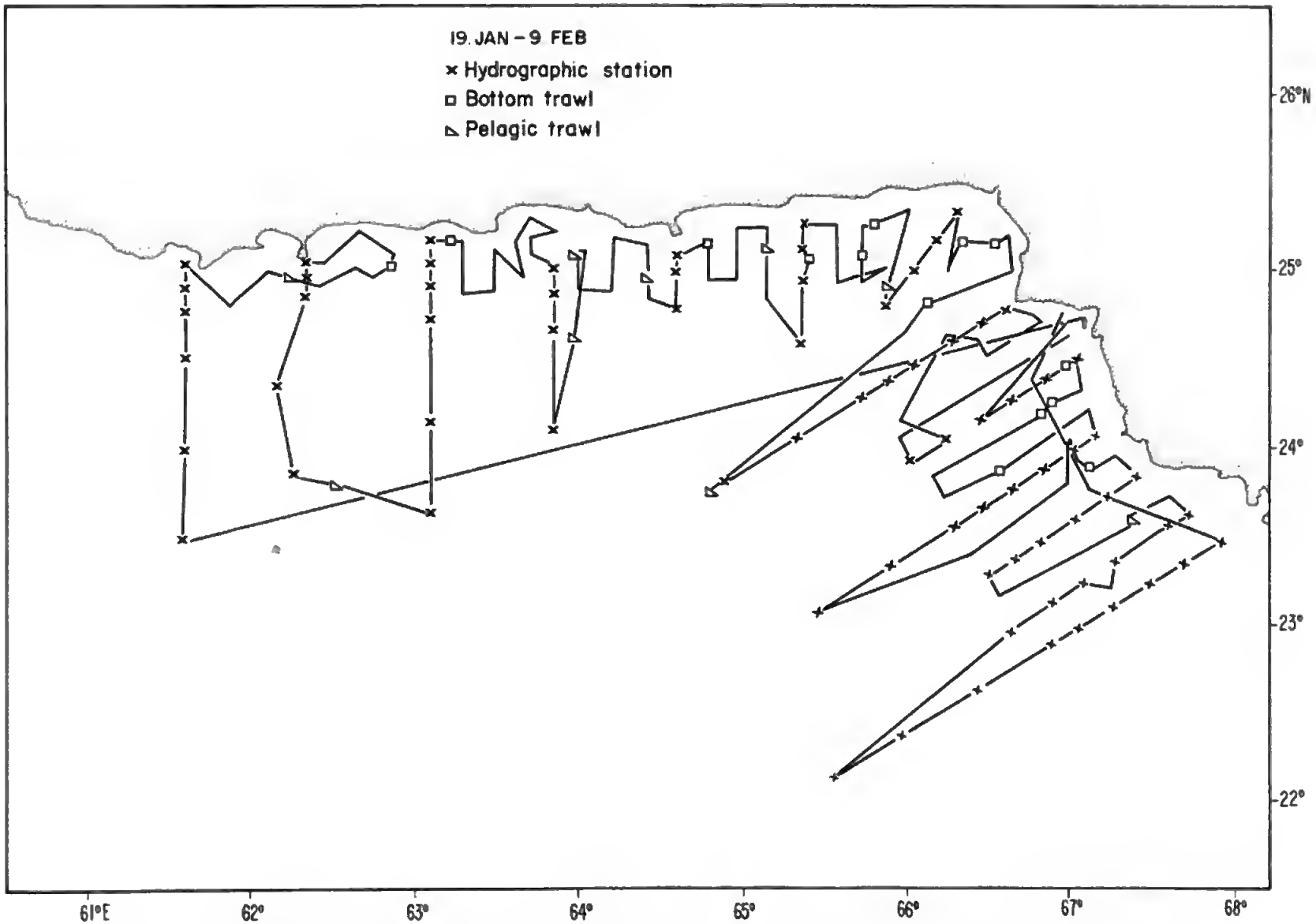

Fig. 12.3 Cruise tracks and station types for study off the coast of Pakistan during 19 January to 9 Feburary 1977. This area was covered five times during the period January - June 1977.

Table 12.1

Estimated abundance of mesopelagic fish in the areas investigated by R/V Dr. FRIDTJOF NANSEN (in million tonnes)
Numbers in brackets are size of the areas in n mi^2 x 10^3
For areas see Fig. 12.1.

Cruise No.	Period	Area A (26.6)	B (27.7)	C (95.0)	D (109.1)	E (30.2)	F (43.6)	G (89.3)	H (37.1)	I (29.5)	Total (488.1)
1.2	Spring 1975	20	8	23	15	12	28	26	10	6	148
3	Autumn 1975	8	6	19	17	12	16	20	6	3	107
4	Spring 1976	13	7	23	15	5	11	31	5	3	113
5	Summer 1976	11	7	17	6	2	4	6	1	2	56
6	Autumn 1976	15	5	20	11	3	4	20	3	3	84
Mean		13	7	20	13	7	13	21	5	3	102

(unpublished) show that about two million tonnes of mesopelagic fish may be present in the area. The highest concentrations (about 10 - 30 g/m^2) were observed just off the shelf. The catch rates were always much lower than in the northern Arabian Sea.

During the summer and autumn of 1978, R/V Dr. FRIDTJOF NANSEN also worked off the Seychelles and off Sri Lanka. The final results of these cruises are not available yet, but a preliminary assessment indicates that the abundance of mesopelagic fish is very low compared to the Arabian Sea.

Nellen (1973) reports studies of eggs and larvae in the Arabian Sea from December 1964 to April 1965. The Myctophidae were the dominant group of fish larva with the Gonostomatidae ranking next. In the Gulf of Oman the Myctophidae amounted to 335 larva/m^2. In the other areas it ranged from 12 to 37 larva/m^2. The Gonostomatidae ranged from 2 to 8 larvae/m^2 (Table 12.3). In the Gulf of Oman and off Pakistan one species, *Benthosema pterotum*, made up the bulk of the samples. The data do not provide any information on seasonal variation.

Fursa (1969, 1973 and 1976) studied fish eggs and larvae in various parts of the Arabian Sea using large, conical ichthyoplankton nets fished in depth strata down to 100 m. The abundance of larvae is reported as number of larva/100 m^3. Supposing that the larvae were distributed in the upper 100 m, this equals larva/m^2 surface area.

Fursa (1969) collected larva along the western shore of the Indian peninsula during the winter (January-March) and summer (June-July) monsoon, finding 14 and 6 larva of mesopelagic fish/m^2 surface area in the two periods, respectively. In waters of depth between 180 and 950 m the abundance was 15 and 10 larva/m^2 and in waters deeper than 1 000 m he got 26 and 19 larva/m^2, in the winter and summer monsoon, respectively (Table 12.3).

Table 12.2

Trawl stations taken by R/V Dr. FRIDTJOF NANSEN
with catch rates of myctophids > 400 kg/hour

St.No.	Date	Area	Trawl	Trawl-depth m	Time	Total catch kg	Catch mycto-phids kg	Myctophids kg/hr	Dominant species
	1975								
168	19.9	F	P	180	day	5 210	5 000	9 400	
219	17.10	C	P	180	day	1 500	1 500	3 000	
234	3.11	C	P	40	night	300	230	400	*B. pterotum*
239	7.11	B	P	250	day	610	600	1 200	*B. pterotum*
	1976								
281	31.1	E	P	85	night	410	405	810	*B. pterotum*
310	22.2	D	P	280	day	2 000	2 000	6 000	*B. fibulatum*
314	26.2	D	P	270	day	250	230	460	*B. pterotum*
319	28.2	A	P	20	night	900	800	1 600	*B. pterotum*
320	29.2	A	P	20	night	1 500	1 500	3 000	*B. pterotum*
325	5.3	A	P	140	day	800	780	1 560	*B. pterotum*
326	5.3	A	P	20	night	450	440	880	*B. pterotum*
327	5.3	A	P	100	day	450	430	860	*B. pterotum*
329	6.3	A	P	20	night	5 000	5 000	10 000	*B. pterotum*
330	6.3	A	P	130	day	650	650	1 300	*B. pterotum*
352	26.3	C	P	90	day	300	200	400	*B. pterotum*
419	25.5	D	KT	200	day	1 500	1 500	3 000	*Diaphus* spp.
427	3.6	C	P	130	day	10 000	10 000	20 000	*B. pterotum*
433	10.6	B	P	100	dawn	1 000	1 000	2 000	*B. pterotum*
434	10.6	B	P	175	day	600	500	1 000	*B. pterotum*
436	13.6	C	P	20	night	300	300	600	*B. pterotum*
448	20.6	A	P	15	night	1 500	1 300	2 600	*B. pterotum*
449	20.6	A	KT	20	night	800	700	1 400	*B. pterotum*
450	20.6	A	KT	30	night	1 500	1 300	2 600	*B. pterotum*
451	20.6	A	P	30	night	500	400	800	*B. pterotum*
469	29.8	B	P	300	day	1 000	1 000	1 000	*B. pterotum*
543	26.10	G	BT	120	night	10 000	9 600	19 000	*B. fibulatum*

P = pelagic trawl (1360 meshes); KT = krill trawl; BT = bottom trawl

Table 12.3

Larval studies in the Indian Ocean
The figures represent larvae/m^2

Author	Period	E. Atrica M	E. Atrica G	G. Aden M	G. Aden G	G. Oman M	G. Oman G	Pakistan M	Pakistan G	India M	India G	Open Ocean M	Open Ocean G
Fursa 1969 *	Jan.-Mar. 1967									6	8		
	Jun.-Jul. 1967									5	1		
Fursa 1973 *	Jan.-Apr. 1969					43	3	20	1				
	Jul.-Sept.1969					4	-	3	-				
	October 1969					4	1	4	1				
Nellen 1973	Dec.-Apr. 1965	12	4	21	4	335	2			37	5	15	8
Fursa 1976 *	August 1971									2	3		
Ali Khan 1976 **	November 1964							44	2				
	March 1967							41	9				
	March 1968							40	4				

* Larva per 100/m^3 = larva/m^2 if they are evenly distributed in upper 100 m

** Mean of stations off or near the 200 m line

M = Myctophidae; G = Gonostomatidae

Fursa (1973) collected larvae off the coast of Pakistan and in the Gulf of Oman. Most stations were in offshore waters. Except a section near the mouth, the Gulf of Oman was only sampled during the winter monsoon, when 46 mesopelagic larvae/m^2 were recorded. Off the coast of Pakistan 21 larvae/m^2 were caught during the winter monsoon, 3/m^2 during the summer monsoon and 5/m^2 between the monsoons (October) (Table 12.3)

Fursa (1976) again collected larvae along the western shore of the Indian peninsula during the summer monsoon. Most samples were taken in shallow waters and no data for distinguishing between those taken in shallow and those taken in deep waters are given. Along the northern part of the coast (north of Bombay) about 8 larva/m^3 were caught, and along the southern part about 3 larvae/m^2 (Table 12.3).

Off the coast of Pakistan, Ali Khan (1976) collected larvae with an Indian Ocean standard net. The sampling was carried out in the winter monsoon periods of 1964, 1967 and 1968. The number of mesopelagic fish larvae caught at stations near or outside the 200 m depth contour amounted to about 40 - 50 larva/m^2 during the three years. Very few larvae were caught at the shallow stations. The data (Table 12.3) seem to suggest that there are more larva during the winter monsoon than during the summer monsoon. The data also indicate that the highest larval concentrations are found in the Gulf of Oman and off Pakistan.

As too little is known about seasonal variation in spawning, fecundity of the species involved and the age of the larvae sampled, it is difficult to interpret the data in terms of fish abundance. They indicate, however, that the mesopelagic fish biomass in the Gulf of Oman and off Pakistan is higher than off northwest Africa (Section 7), while the other parts of the Arabian Sea may have densities similar to those off northwest Africa.

Synthesis of abundance estimates

Acoustic estimates, catch rates in commercial trawls and larval sampling all show that mesopelagic fish biomass is very high in the north Arabian Sea. Larval sampling indicates that the abundance may be similar along the western coast of India, but the information from that area is not as good. South of Somalia and in offshore areas the abundance is much lower.

The estimates given in Table 12.4 are based on the DR FRIDTJOF NANSEN surveys for areas 1 and 4. For area 2, larval abundance is compared with that in area 1, and based on this ratio a stock estimate is derived. For areas 3 and 5, the estimates are based on catches from micronekton nets, although the low values seem to be confirmed by acoustic studies in parts of these areas

Nearly one half of the mesopelagic fish biomass recorded from the western Indian Ocean is found in nearshore areas of the Arabian Sea (Table 12.4). It is, however, important to note that both the results of the DR FRIDTJOF NANSEN and those of the Regional Fishery Survey and Development Project from the Gulf of Oman suggest that there may be large variations in abundance in the north Arabian Sea. More work is needed to assess the short-term and long-term variation in this area.

Table 12.4

Abundance estimates for various parts of the Western Indian Ocean
For areas see Fig. 12.4

Area No.	Size of area $m^2 \times 10^{11}$	Biomass g/m^2	Stock Tonnes $\times 10^6$
1	17	60	100
2	5	30	15
3	95	0.5	50
4	3.5	6	2
5	184	0.5	90
	304.5		257

Depth distribution

In the neritic areas of the Arabian Sea a very dense mesopelagic fish layer was usually observed between about 150 and 200 m and a more diffuse one between 250 and 350 m (Fig. 12.5). During the night most of the fish concentrated in the upper 50 m.

In offshore and southern parts of the Arabian Sea a DSL was usually observed at 250-350 m and sometimes an additional one was found between 350 and 500 m. This larva layer, or part of it, was sometimes observed in the same depth during the night, too (Gjøsaeter, 1978a).

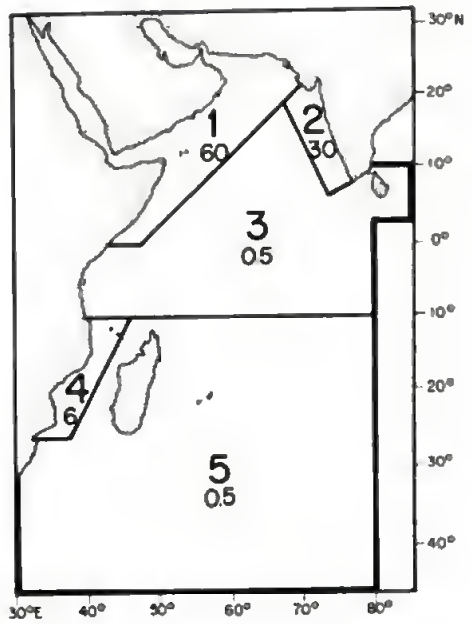

Figure 12.4 Subareas of the W.Indian Ocean used in the biomass assessment (Table 12.4). The smaller figures indicate the biomass in g/m^2

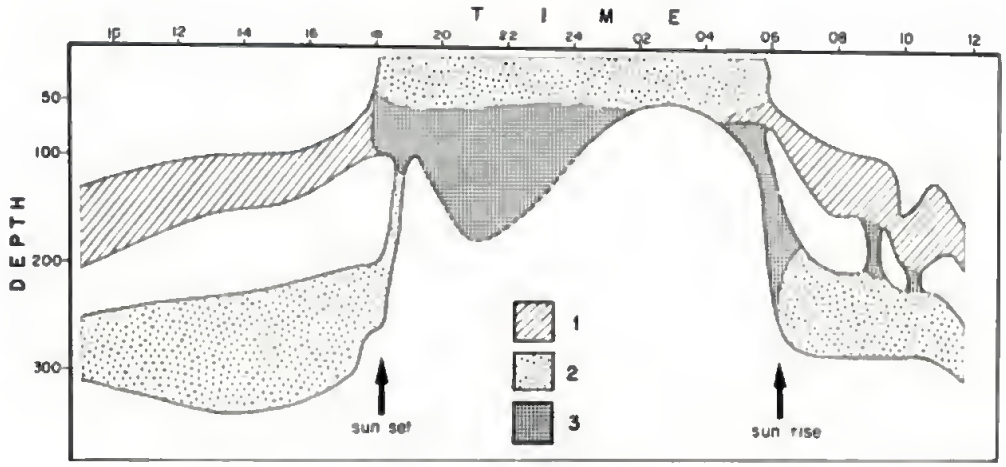

Figure 12.5 Vertical migration of DSLs as observed with 38 kHz echosounder during a diurnal station in the Gulf of Oman taken by R/V Dr. FRIDTJOF NANSEN, March 1976: 1) schools and very dense aggregations, 2) dense recordings, 3) scattered recordings. (From Gjøsaeter 1978a)

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Further to the south, Bradbury *et al.* (1971) observed the main DSL from 300 - 350 m downward. Sometimes two bands were observed, the lower one centred at or below 500 m.

Species composition

In the highly productive areas of the Arabian Sea *Benthosema pterotum* was the dominant species, but *B. fibulatum*, *Hygophum proximum*, *Bolinichthys longipes* and *Diaphus thiollierei* were also abundant (Nafpaktitis and Nafpaktitis, 1968; Gjøsaeter, 1978a; Nafpaktitis, 1978).

Further to the south the diversity was higher. In equatorial waters *Notolychnus valdiviae* seems to be important in offshore areas (Bradbury *et al.*, 1971).

In nearshore waters off Mozambique, *Benthosema fibulatum*, *Diaphus perspicillatus* and *D. watasei* are most frequently caught.

Life history

Aspects of the life history of the two dominant species from the Arabian Sea, *Benthosema pterotum* and *B. fibulatum*, were studied by Gjøsaeter (1978a).

B. pterotum grow to a maximum size of about 50 mm, but specimens larger than 45 mm are rare. Rings in the otoliths, which are presumed to be growth zones, indicate that the maximum size is reached within one year. Reproduction is continuous but with maxima in March-June and September-November (Makhdoom, in prep.). Feeding generally takes place during the early evening and copepods and various crustacean larvae seem to be the dominant food items.

B. fibulatum reach a maximum size of about 100 mm, but specimens larger than 80 mm are uncommon. Rings in the otoliths suggest that the species has a one-year life cycle. Sexual maturity seems to be reached at a length of about 40 mm.

Diaphus watasei and *D. coruleus* are among the largest myctophid species known, both reaching a size between 150 and 300 mm. Adults of both species are usually caught at or near the bottom both day and night (Nafpaktitis, 1978; Gjøsaeter, 1978 and unpubl.).

13. EASTERN INDIAN OCEAN

The available information on the abundance of mesopelagic fish in this area is very sparse, especially in the subantarctic area. The distribution of biomass could therefore only be estimated from scattered micronekton net data. The area was divided into four subareas I - IV based on net catches and the distribution of primary production and zooplankton abundance. The total biomass was estimated from converted IKMT-10 ft values for each area. The results of some zoogeographical surveys are also available, which are useful as indicators of species composition.

Abundance

Legand (1969) reported the seasonal variation in biomass of micronektonic animals at ten stations along 110°E between 9°S and 32°S, based on IKMT-5 ft samples collected at night in the upper 200 m layer. The sampling was done every month from August 1962 to August 1963, except December. Annual mean fish biomass is reported to account for 79% of micronekton biomass in dry weight, but seasonal fluctuations were reported only for the total micronekton. Among his results, the following are thought important for the purposes of this review:

1. The biomass of the micronekton showed a smaller variation both chronologically and geographically than did the plankton.

2. Total micronekton biomass along 110°E between 9°S and 32°S decreased from January to March.

A calculation of fish biomass from the annual mean of the micronekton biomass at nine stations is shown in Table 13.1. For the calculation, the annual mean percentage of fish biomass in the total micronekton biomass was taken to be 79%, the conversion ratio from dry weight to wet weight as 4.3, and the volume of water filtered per standard haul as 19 290 m^3, all of which were measured or assumed by him. The efficiency (catchability coefficient) of the IKMT-5 ft was assumed to be 0.8.

Table 13.1

The relative abundance of micronekton in the upper 210 m layer at night along 110°E between 9°S and 32°S in the southeastern Indian Ocean
The values were read from Legand (1969, Fig. 3)

	9°S	9°30'S	12°S	15°S	18°S	21°S	24°S	27°S	30°S	32°S
Micronekton biomass (g dry wt/haul)	9.1	8.2	6.6	5.9	5.5	4.9	7.1	6.9	5.5	6.7
Fish biomass (g dry wt/haul)	7.2	6.5	5.2	4.7	4.3	3.9	5.6	5.5	4.3	5.3
Fish biomass (g wet wt/haul)	31.0	28.0	22.4	20.3	18.5	16.8	24.1	23.7	18.5	22.8
Fish biomass (g wet wt/m^2)	0.40	0.38	0.30	0.28	0.25	0.23	0.30	0.30	0.25	0.30

The abundance of micronektonic fish was measured in the upper 1 000 m by a ring net (ORI-net) along 86°E latitude between 16°N and 20°S in February - March 1977 (Kawaguchi, unpublished). The results are shown in Fig. 13.1 together with those of Legand (1969) and the distribution of annual primary production from FAO (1972).

Synthesis of abundance estimates

Reliable data are very few for this area, but we may safely estimate the lower limit of the order of magnitude of biomass by the following considerations and procedures. The abundance estimated from ORI-net data collected in February - March is thought not higher than the annual mean, according to Legand's (1969) results on seasonal fluctuation of micronekton biomass. The abundance of mesopelagic fish will show a less variable geographical distribution than primary production, owing to the mobility of the fish in the mesopelagic zone, which is itself a more stable environment than the epipelagic zone. With these features in mind, we can derive the following patterns from Fig. 13.3. In the area of the lowest primary production (< 100 mg C/m^2/d), the biomass of mesopelagic fish is usually low (0.5 ~ 0.8 g wet wt/m^2). Two high values (1.5 and 1.6 g/m^2) were also obtained in this unproductive area near the rather complicated contour line of primary production, but this kind of anomaly in the distribution of primary production and mesopelagic fish biomass seems natural, if the strong seasonal change of the physical environment in the epipelagic zone caused by the monsoon in this area, and the swimming ability of the fish, are taken into account. Legand's results show that the annual mean biomass in the upper 200 m layer at night is fairly uniform in the area where 100 - 250 mg C/m^2/d primary production is observed, and higher in the area where more than 250 mg C/m^2/d is measured.

In consideration of the foregoing we divided the eastern Indian Ocean into four subareas as shown in Fig. 13.2. The value 0.7 g/m^2 for the area of lowest production (subarea IV) was obtained by averaging the six ORI-net values (0.5 - 0.8 g/m^2). All the other ORI-net values, 0.9 ~ 3.0 g/m^2 were averaged to obtain the value (1.5 g/m^2) for subarea II. The values in subarea I and III were assumed to be 1.2 and 0.8 times as large as that in subarea II. All these values, based on the ORI-net, were converted to equivalent IKMT-10 ft values by using the factor 2.6, obtained in the Western North Central Water area (see Section 14, Northwest Pacific).

The highest value, for subarea I, is comparable to that of the Kuroshio area north of its axis (transitional zone), and the lowest value, for subarea IV, to that of the central water area of the Northwest Pacific. The estimate for each subarea is presented in Table 13.2. In total the biomass of mesopelagic fish is estimated at 92.9 x 10^6 tonnes on the basis of IKMT-10 ft values.

Table 13.2

Estimated total biomass of the mesopelagic fishes in each subarea of the eastern Indian Ocean

Subareas	Size of subarea m^2 x 10^{11}	Biomass (g/m^2) ORI-net	IKMT-10 ft*	Stock (tonnes x 10^6 from IKMT-10 ft values)
Subarea I	34	1.8	4.7	16
II	75	1.5	3.8	29
III	122	1.2	3.1	38
IV	59	0.7	1.8	11
Total	290			94

* Converted from the ORI-net data

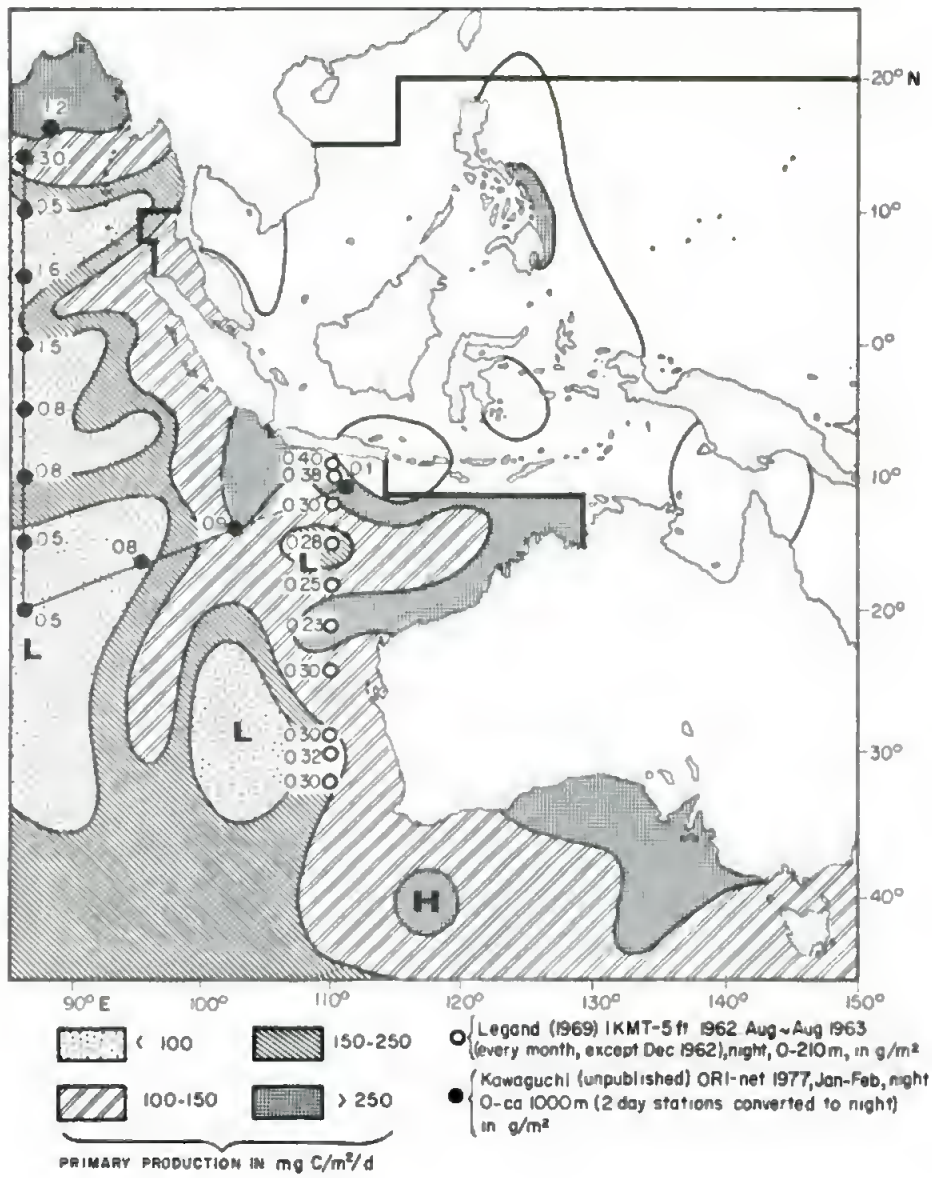

Fig. 13.1 Distribution of the fish micronekton biomass measured by IKMT-5 ft and ORI-net, and its relation to the distribution of primary productivity.

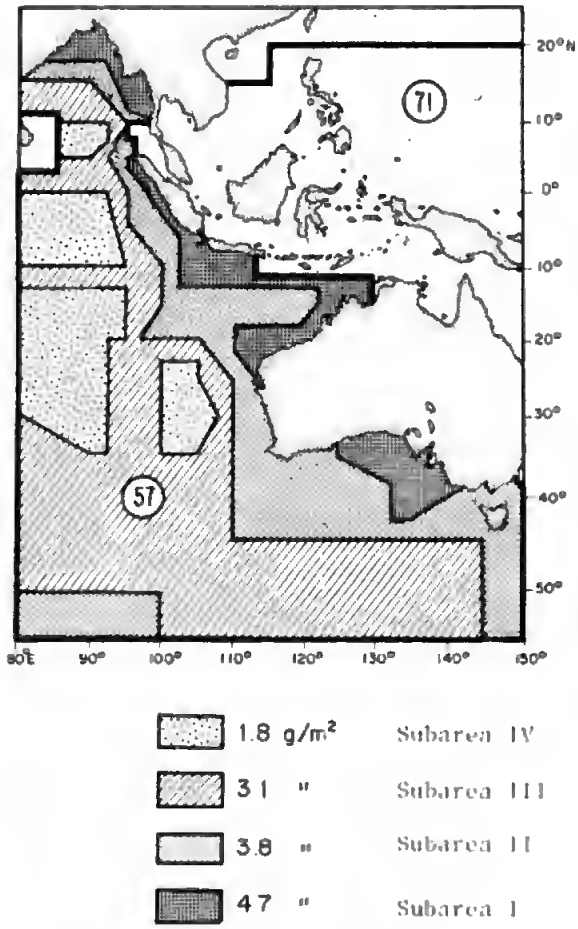

Fig. 13.2 The four subareas and values used for the estimation of total biomass in the eastern Indian Ocean.

Depth distribution

Reliable data based on opening-closing nets or acoustic instruments are not yet available for this area. In future the vertical distributional pattern of mesopelagic fish should be studied in relation to the oxygen minimum layer prevailing in the mesopelagic zone of the northern Indian Ocean.

Species composition

Based on the taxonomical and zoogeographical works by Bekker (1964), Mukhacheva (1972, 1974, 1976), Gorbunova (1972), Kawaguchi *et al.* (1972) and Nafpaktitis (1978), the following species are thought to be common in the eastern Indian Ocean. There remains much to be learned about the quantitative species composition in this area.

Gonostomatidae: *Cyclothone alba, C. pseudopallida, C. pallida, C. microdon, C. acclinidens, Gonostoma elongatum, G. atlanticum, Vinciguerria nimbaria, Bonapartia pedaliota, Margrethia obtusirostra.*

Myctophidae: *Benthosema suborbitale, Diogenichthys atlanticus, Hygophum proximum, Myctophum nitidulum, M. spinosum, Symbolophorus evermanni, Centrobranchus nigroocellatus, Notolychnus valdiviae, Lampanyctus steinbecki, L. alatus, L. nobilis, Lepidophanes longipes, Ceratoscopelus warmingi.*

Life history

No available data.

14. NORTHWEST PACIFIC

This area can be divided into three subareas according to the distribution of biomass densities, i.e. the subarctic, Kuroshio system, and Western North Pacific Central Water areas. Most investigations have been carried out with micronekton nets and some information is also available from larva surveys, zoogeographical surveys and accidental catches in commercial fisheries. No acoustic data are available.

Abundance

Aizawa and Marumo (1967) and Murano *et al.* (1976) reported the vertical distribution of zooplankton and micronekton biomass in the upper 1 000 m of the Kuroshio Current area off central Japan. They used a 160 cm ring net (ORI-net) equipped with an opening-closing device and towed horizontally to collect samples from discrete depth layers. Using tbe same type of net towed obliquely in the upper 1 000 m layer, Kawaguchi (1973, unpubl.) investigated the geographical distribution of the micronektonic fish abundance in the western north Pacific between 20°N and 45°N. According to the biomass distribution, he divided the investigated area into four subareas: the subarctic area, the Kuroshio areas north and south of its axis, and the Western North Pacific Central Water area. The estimated values obtained from these surveys are listed in Table 14.1. The night catch data derived from the discrete depth sampling agree well with those obtained in oblique tows in the Kuroshio area north of its axis.

Parin *et al.* (1977) estimated mesopelagic fish biomass in the western tropical Pacific and defined three areas according to the observed distribution of abundance, i.e. the equatorial, the Kuroshio and the central water areas. The Kuroshio area as defined by these authors corresponds to the Kuroshio area south of its axis as described by Kawaguchi (unpubl).

Acoustic data are not available on mesopelagic fish abundance in this area. During the course of an investigation to find the spawning ground of the Japanese eel, Ozawa and Tsukahara (1971), Tsukahara *et al.* (1974), Kawaguchi (1974), Ozawa (1976) and Matsui *et al.* (1976) reported the dominance of mesopelagic fish larvae in the Kuroshio and central water areas. Similar results have been obtained by Melchikova (1969), Odate (1961) and Hattori (1964) off Japan. But these data are not suitable for estimating absolute biomass.

Synthesis of abundance estimates

Considerable differences in sampling efficiency have been observed between day and night tows and between ORI-net and IKMT tows. Therefore, we adopt here the average biomass estimated from night catches by both nets for calculating a lower limit of the true biomass. In Table 14.2 IKMT values in the Oyashio area and the Kuroshio area north of its axis were calculated from the ORI-net data by using the conversion ratio 2.6 from the central water area where data for both net types are available. The observed conversion ratio is much higher in the Kuroshio area than in the central water (3.9 vs. 2.6), but the IKMT data of Parin *et al.* (1977) for the Kuroshio area south of its axis (on which the higher ratio is based) is possibly higher than the average, since their sampling stations were located in the comparatively productive area near oceanic islands such as the Ryukyu and Bonin Islands. Therefore, we adopted here the lower ratio from the central water to avoid an over-estimation.

For the calculation of total biomass, the northwest Pacific area was divided into thres subareas based on observed biomass density: these areas generally conform to the three major water masses; subarctic waters, waters of the Kuroshio system and Western North Pacific Central Water, as defined by Sverdrup *et al.* (1946), although their boundaries are slightly shifted in accordance with the abundance of mesopelagic fish, zooplankton or primary production, as shown in Fig. 14.1. To calculate the total biomass in each subarea, we applied the value of the Oyashio area to the subarctic area (Table 14.3). The value for the waters of the Kuroshio system was obtained by averaging the values on the two sides of the Kuroshio axis.

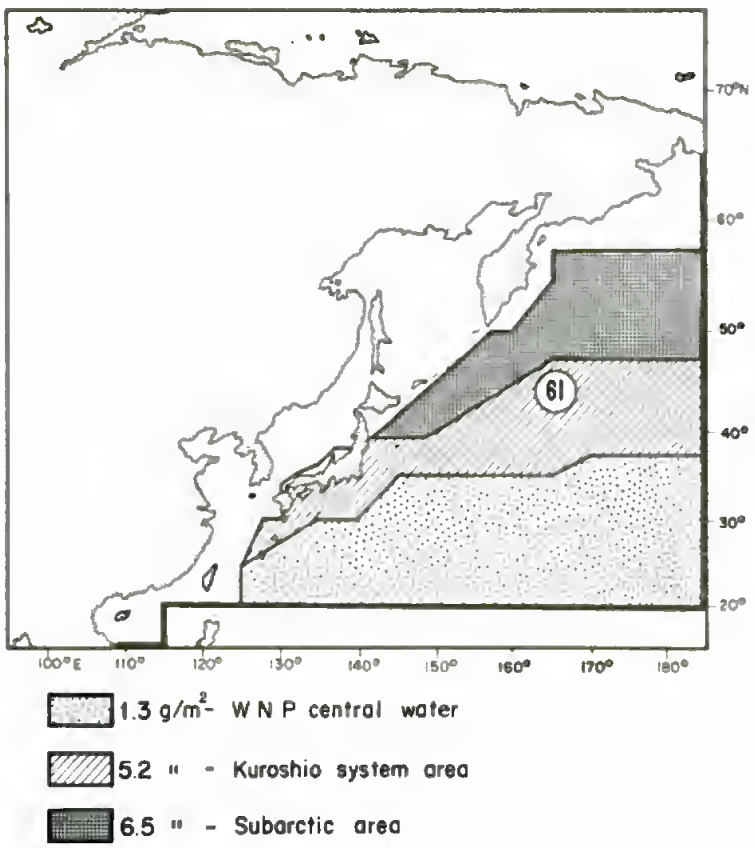

Fig. 14.1 The three subareas and values adopted for the total biomass estimation of mesopelagic fishes in the Northwest Pacific.

Table 14.1

Biomass data obtained by micronekton nets in the Northwest Pacific

Sources	Biomass g/m^2	No.of samples or series	Night catch or day catch	Nets and towing method	Sampling depth	Sampling locality
Aizawa and Marumo (1967)	2.1	4	N	ORI-net* horizontal tow	0~ 1000 m	ca. 34°41.5'N ca. 140°00.0'E
Murano *et al.* (1976)	1.9	1	N	ORI-net horizontal tow	0~ 1000 m	ca. 34°45'N ca. 139°35'E
	1.3	1	D			
Kawaguchi (1973)	2.4 ± 0.8	7	N + D	ORI-net oblique tow	0~ ca. 1000 m	Kuroshio area north of its axis
	1.6 ± 0.4	7	N + D	ORI-net oblique tow	0~ ca. 1000 m	Kuroshio area south of its axis
Kawaguchi (unpubl.)	2.5 ± 1.2	4	N	ORI-net oblique tow	0~ ca. 1000 m	Oyashio area north of 40°N, west of 150°E
	1.9 ± 0.6	4	D			
	2.1 ± 1.0	11	N	ORI-net oblique tow	0~ ca. 1000 m	Kuroshio area north of its axis (30°~40°)
	1.6 ± 0.7	13	D			
	1.2 ± 0.8	15	N	ORI-net oblique tow	0~ ca. 1000 m	Kuroshio area south of its axis (20°~30°N)
	1.2 ± 0.8	14	D			
	2.5 ± 1.2	6	N	ORI-net oblique tow	0~ ca. 1000 m	Sagami Bay off central Japan
	1.2 ± 0.6	15	D			
	0.5	1	N	ORI-net oblique tow	0~ ca. 1000 m	Western North Central Water
	0.6 ± 0.1	2	D			
Parin *et al.* (1977)	4.7**	3	N	IKMT-10 ft horizontal tow	0~ 1000 m	Kuroshio area south of its axis
	1.3**	10	N	IKMT-10 ft horizontal tow	0~ 1000 m	Western North Pacific Central Water

* ORI-net: a 160 cm ring net
** read from Fig. 41 of Parin *et al.* (1977)

Table 14.2

The average night catch by ORI-net and IKMT-10 ft in the major three subareas of the Northwest Pacific. Data in parentheses were calculated from the ORI-net data by the conversion ratio 2.6

Areas	Method		Conversion Ratio
	ORI-net	IKMT-10 ft	
Subarctic area	2.5 g/m^2	(6.5) g/m^2	(2.6)
Kuroshio system area			
north of its axis	2.1	(5.5)	(2.6)
south of its axis	1.2	4.7	3.9
average	1.7	5.2	4.2
Western North Pacific Central Water	0.5	1.3	2.6

Table 14.3

Estimated total biomass of mesopelagic fish in the Northwest Pacific, based on ORI-net and IKMT data

Subareas	Size of area $m^2 \times 10^{11}$	Biomass g/m^2		Stock tonnes $\times 10^6$	
		ORI-net	IKMT	ORI-net	IKMT
Subarctic area	24	2.5	6.5	6	16
Kuroshio system area	41	1.7	5.2	7	21
Western North Pacific Central Water	90	0.5	1.3	5	12
Total				18	49

The results, presented in Table 14.3, show the estimated total biomass in the northwest Pacific to be 18 million tonnes according to ORI-net data and 49 million tonnes according to IKMT data. The two different results are presented here to show the difference in catching ability of the two micronekton nets towed in different ways.

The southern Japan Sea is inhabited by only one mesopelagic species, *Maurolicua muelleri* which has been known to form dense schools near the edge of the insular slopes (Okiyama, 1971). Assuming its total range to be the long narrow area 10 km x 600 km along the edge of shelves, and its density to be the same (5.2 g/m^2) as in the Kuroshio system, the total biomass is 3.1×10^4 tonnes. This value seems rather low but its availability as a potential resource should be stressed here.

The Okhotsk Sea is inhabited by *Stenobranchius nannochir* and *Lampanyctus jordani* and the Bering Sea also by several species (Kulikova, 1954; Bekker, 1967). But these areas, which are closed by ice in winter, were excluded from the present estimation because of the lack of any abundance data.

Depth distribution

Aizawa and Marumo (1967) reported a bimodal vertical distribution of mesopelagic biomass at night with the maximum biomass in the upper 200 m layer and another peak in the 800 - 1 000 m layer. During the day, the peak was observed in the 400 - 600 m layer where the minimum biomass was observed at night. They also pointed out the possible recruitment of biomass from the deeper layer into the 800 - 1 000 m layer at night. In the same area, Murano *et al.* (1976) observed the peak biomass in the upper 100 m layer at night and in the 500 - 700 m layer during the day, although the bimodal vertical distribution was not so clear as observed by Aizawa and Marumo (1967).

Parin *et al.* (1977) found a similar bimodal distribution in the Kuroshio, the Southeast Asian Seas, the equatorial current and the Western North Pacific Central Water area. This bimodality may result from the diurnal recruitment of biomass into the upper 100 m layer mainly from the 300 - 600 m layer while the considerable biomass of non-migratory species remains below 500 m.

Gonoatoma gracile, one of the dominant species of mesopelagic fish in the Kuroshio area, is known to occur at maximum density in the 300 - 700 m layer both day and night, with a small amount of its biomass migrating up to the shallower layers, probably following some vertically migrating prey.

The diel migration of *M. muelleri* has been studied by acoustics on the insular shelves and slopes of the southern Japan Sea (Kawaguchi, 1967). It is known to migrate to the upper 100 m at night and spend the day near the bottom.

Species composition

Zoogeographically, the Northwest Pacific can be divided into four subareas: the subarctic area, the subtropical area, the transitional area between the above two and the slope water area along Japan south of 40°N.

In the subarctic area, mainly north of 40°N with its boundary shifted northward in the offshore area, the most abundant species are the myctophids *Tarletonbeania crenularis, Symbolophorus californiensis, Diaphus theta, Stenobrachius nannochir, S. leucopsarus* and *Lampanyctus jordani*, (Kulikova, 1960, 1961; Bekker, 1964, 1967). The biomass of the surface migrating myctophid species, *S. californiensis* and *T. crenularis*, which are abundantly collected in night surface tows from the side of the ship tends to be underestimated in the data obtained by oblique tows from the stern, mainly owing to disturbance by the ship. The nonmigratory gonostomatid species *Cyclothone atraria, C. pallida, C. pseudopallida, C. alba* and *Gonoatoma gracile* also commonly occur in this area, although the Bering Sea is inhabited by only one species, *C. atraria* (Mukhacheva, 1954, 1964, 1972, 1974). It should be noted that the subarctic area is not inhabited by vertically migrating gonostomatid species.

In the transitional area around 40°N, species of both subarctic and subtropical regions occur, and the endemic species *Protomyctophum crockeri* and *Notoscopelus japonicus* are also abundant. *N. japonicus*, a large myctophid reaching more than 15 cm, is rarely collected in micronekton nets but its high abundance in this area may be inferred from its frequent occurrence in the stomachs of fur seals wintering in the transitional area off Japan (Japan Fisheries Agency, 1967).

In the subtropical area, including the Kuroshio system and the central water areas, the data on surface-migrating myctophids have been collected by night surface tows of larva nets (Sarenas, 1954; Odate, 1961; Hattori, 1964; Bekker, 1964; Kawaguchi and Aioi, 1972; Kawaguchi *et al.*, 1972). The principal surface-migrating species are listed in Table 21.3. Concerning the midwater migrants and non-migrants, the data have been obtained mainly by oblique or horizontal tows of IKMT and ring trawls. The following species usually dominate the catch in number or wet weight.

Myctophidae: *Diogenichthys atlanticus, Benthosema suborbitale, Diaphus kuroshio, D. schmidti, Notoscopelus respelendens.*

Gonostomatidae: *Vinciguerria nimbaria, Gonostoma gracile, Cyclothone atraria, C. alba, C. pseudopallida, C. pallida.*

The slope water area, south of 40°N off Japan, is inhabited by several species of medium-sized and large myctophids (Kosaka *et al.*, 1967; Kawaguchi, 1976; Kawaguchi and Shimizu, 1978). The larger species, reaching 120 mm or more, are often taken in commercial midwater trawls fishing sergestid shrimp in Suruga Bay off central Japan and in bottom trawls in commercial fisheries carried out on the insular slopes off central and southern Japan. But they are rarely collected by micronekton nets, which they avoid. The fishermen locally consume some of these slope water species, *Diaphus watasei, D. suborbitalis* and *D. sagamiensis*, although they are always caught accidentally and not landed for sale. In view of their commercial potential, the main slope water species are listed below (Kawaguchi, 1976):

Larger myctophid species:

Diaphus watasei, D. sagamiensis, D. gigas, D. adenomus.

Medium and smaller myctophid species:

Benthosema pterotum, Diaphus suborbitalis, D. garmani.

Life history

Myctophum affine (= M. nitidulum) is one of the dominant surface migrating myctophids off Japan (30°~ 40°N), and its life history has been studied by Ogawa (1961), Odate and Ogawa (1961) and Odate (1966). The species is known to spawn during spring and summer. The young reach ca. 45 mm standard length one year after hatching, ca. 60 mm after two years and ca. 70 mm after three years. The spawning group is reported to be three years or older, but the total lifespan is unknown. The fecundity was counted at about 8 000. Mature adults seem to stop the diel vertical migration to surface layer, as their frequency of occurrence in night surface tows is remarkably low during the spawning season.

Diaphus suborbitalis, which is the abundant slope water species in Suruga Bay off central Japan, spawns mainly in summer. The juveniles, 15 - 20 mm in autumn, rapidly grow to about 50 mm SL by the next summer, and after that the growth rate gradually decreases. The following von Bertalanffy growth equation agrees well with the observed growth:

$$l_t = 60.03 \{1 - \exp [- 0.11 (t + 2.57)]\}$$

where l_t = size at age t

t = age in months

The maximum size observed was 67 mm SL at the age of 2.5 years (Go *et al.*, 1977b). Knowledge of spawning behaviour is still insufficient for this species.

Gonostoma gracile, one of the most abundant gonostomatids in the Kuroshio area (Kawaguchi, 1973), spawns mainly in winter and spring. The young reach maturity as males about one year after hatching at a size of 50 - 60 mm SL, and then breed with two-year old or older females. After breeding, mainly in summer, the males change sex to female and spawn as such in the next breeding season. The maximum size observed is 120 mm SL. The female may survive for at least two years (Kawaguchi and Marumo, 1967).

Maurolicus muelleri is the only micronektonic fish species from the Pacific which has succeeded in establishing itself in the Japan Sea, and it predominates there. Its spawning is intense in spring, the average fecundity being about 300. The eggs float in the 10-75 m layer, and the larvae have been observed in the 50 - 70 m layer, although no sampling was done below 75 m (Nishimura, 1959; Okiyama, 1971). Annual fluctuations in the abundance of *M. muelleri* eggs and larvae are much smaller than those of three species of clupeoids in the area, namely *Sardinops melanosticta*, *Etrumeus microps* and *Engraulis japonica* (Okiyama, 1971).

15. NORTHEAST PACIFIC

This area can be divided into two subareas: the subarctic and transitional areas. These areas correspond to the eastward extension of the subarctic area and the Kuroshio area north of its axis from the adjacent Northwest Pacific. Extensive surveys have been done with micronekton nets in the transitional region, and there are also data from acoustic and larva surveys, but the latter are insufficient for abundance estimation.

Abundance

Based on IKMT-6 ft sampling in the upper 225 m layer at night, Aron (1962) reported the relative abundance of several dominant species of mesopelagic fish in a wide area of the Northeast Pacific, including the southern Bering Sea. The results can be summarized as follows: 1) Biomass density in the southern Bering Sea was at least as great as in the subarctic area south of the Aleutian Islands. 2) A clear boundary was observed corresponding roughly to the 45°N line in the offshore area. The quantitative change was by a factor of 10 and the qualitative change was such that there was very little species overlap between the two sides of the boundary, at least among the animals identified to species. Considering these results together with similar patterns in the distribution of zooplankton and primary production (FAO, 1972), we can divide the area into the two subareaa mentioned above, namely the subarctic and transitional areas (Table 15.1).

Table 15.1

Total estimated biomass based on micronekton net catches in the Northeast Pacific

Subareas	Size of area x 10^{11} m^2	Biomass density (IKMT-6ft) g/m^2	Stock 10^6 tonnes
Subarctic area	34	4.5	15
Transitional area	32	3.6	12
Total			27

Pearcy and Laurs (1966) reported the biomass of mesopelagic fish based on 152 collections made by IKMT-6 ft in the transitional area off Oregon (44° 39'N, 125° 15'W), almost at the boundary of the two subareas defined above. The average number and wet weight per m^2 in the 0 - 100 m layer were:

	Day	Night
catch in number (ind./m^2)	1.1	1.5
catch in wet weight (g/m^2)	2.4	3.6
wet weight per individual (g)	2.2	2.4

Furthermore, the night biomass in the 150 - 500 m and 500 - 1 000 m layers was measured as ca. $4g/10^3$ and ca. $1.4g/10^3m^3$, respectively (Pearcy and Laurs, 1966, Fig. 3). Assuming that the biomass was distributed evenly in the 150 - 500 m layer, these values imply a density of 1.9 g/m^2 in the 200 - 1 000 m layer.

Pearcy (1976) studied the seasonal change in biomass in the uppermost 200 m layer at night at six stations located 28, 46, 84, 120, 157 and 300 km off Oregon along ca. 44° 39'N latitude, collecting 243 samples with IKMT-10 ft. A seasonal inshore-offshore shift in biomass was observed and related to seasonal changes in upwelling in the area. But on the average, biomass in the area more than 84 km offshore was ca. 3.1 g dry weight (read from his Fig. 4) per 10 m^2 in the 0 - 200 m column. This value can be converted into a wet weight of 1.4 (1.2 - 1.8) g/m^2 in the 0 - 200 m column by the conversion ratio 0.23 ± 0.06 which was measured for the fish in the area surveyed.

Acoustic surveys have been restricted to the qualitative features of the DSL and its composition (Taylor, 1968; Pearcy and Mesecar, 1971), and are insufficient for abundance estimates. But the swimbladder morphology of some mesopelagic fishes was studied in relation to buoyancy by Butler and Pearcy (1972), and in relation to sound scattering by Capen (1967), and their findings show that these species will contribute greatly to acoustic abundance in the region. Among their results, it should be noted that *Stenobrachius leucopsarus*, the most abundant species in this area, the juveniles (less than 30 mm in standard length) have a gas-filled swimbladder, but that of adults is regressed and surrounded by fatty tissue. In this context, Pearcy and Mesecar (1971) pointed out in their study on seasonal variation of biomass that the decrease in biomass offshore was correlated with an increased recruitment of small *S. leucopsarus* with gas-filled bladders. The sound scattering strength offshore, therefore, may be higher during winter than summer, even though the total biomass is lower in winter. In the subarctic area of the Northeast Pacific no quantitative data on biomass are available, and it was assumed for calculations in this paper that relative densities were similar to those in the Northwest Pacific, as explained in the next section.

Synthesis of abundance estimates

Clarke (1973), Atsatt and Seapy (1974), and Pearcy *et al.* (1977) reported no significant day-night differences in IKMT catches, but Pearcy and Laurs (1966) did.

In this paper night catch data are adopted, considering the possibility of enbanced visual avoidance of the trawl during daylight hours. The value reported by Pearcy and Laurs (1966), 3.6 g/m^2 in the 0 - 1 000 m layer, is based on 90 samples from various seasons and thought to represent a reliable average measure of density by IKMT in the transitional waters off Oregon. Another average value by Pearcy (1976), 1.35 g/m^2 in the upper 200 m (read from his Fig. 3) is based on 150 samples collected during the study on seasonal offsbore-nearshore variation of biomass off Oregon. This may also be reliable as an average value for the area. If the 1.9 g/m^2 in the 200 - 1 000 m layer at night derived above is added to this value, the biomass is estimated as 3.3 g/m^2 in the 0 - 1 000 m layer, which agrees well with the 3.6 g/m^2 measured by Pearcy and Laurs (1966).

According to Patullo and Lorz (unpubl. indirectly cited from Pearcy, 1978), the ocean off Oregon is a transitional region. The water at 200 - 1 000 m depth consists of modified subarctic water, varying from about 55% to 78% subarctic from 85 to 120 km off the coast. Therefore, tbe density estimated above (3.6 g/m^2) was adopted for calculating the total abundance of mesopelagics in the transitional subarea.

There is no measured value of density in the subarctic area and it was, therefore, calculated from the value for the transitional area by the conversion ratio 1.25. This ratio was obtained from the neighbouring Northwest Pacific, where the conversion ratio can be derived from the ORI-net catches in both areas.

With mean densities of 4.5 g/m^2 in subarctic waters and 3.6 g/m^2 in the transitional area, the total biomass in tbe Northeast Pacific was estimated at 27 x 10^6 tonnes as shown in Table 15.2.

Table 15.2

Average catches of mesopelagic fishes (No. per $10^5 m^3$) in daytime opening-closing IKMT-MPS net tows in the upper 500 m off Oregon. From Pearcy (1977)

Species	Cruise (Year and Month) 6911	7011	7107	7206	7209	7211	7302	7306
Stenobrachius leucopsarus	161.0	158.2	68.7	66.7	9.6	32.9	8.1	18.8
Diaphus theta	22.7	78.1	12.8	23.1	8.2	25.2	11.3	17.6
Tarletonbeania crenularis	3.3	103.7	17.9	7.8	2.3	7.0	3.5	8.6
Tactostoma macropus	3.3	1.3	35.9	13.6	8.8	4.0	2.9	4.5
Protomyctophum thompsoni	9.9	21.5	12.4	7.2	12.1	6.3	1.7	8.3
Lampanyctus ritteri	3.8	12.1	1.7	6.2	2.7	4.3	0.8	0.7
Cyclothone atraria	0	0	14.9	0.3	0.4	2.7	2.0	4.5
Protomyctophum crockeri	1.4	0	0.4	1.2	0.4	0	0	0
Bathylagus pacificus	0	0	4.3	0.3	0	0.3	0	0
Lampanyctus regalis	2.8	0	1.7	0	0	0.3	0	0.7

Depth distribution

Pearcy and Laurs (1966) reported the vertical distribution and migration of mesopelagic fishes off Oregon, based on samples collected in the 0 - 150 m, 150 - 500 m and 500 - 1000 m layers during daylight and darkness. The biomass was larger during the day than the night at intermediate depths of 150 - 500 m, whereas the opposite was true in the upper 150 m (Fig. 15.2). No day-night difference was observed in biomass in the 500 - 1 000 m layer, where catches were uniformly low.

Pearcy *et al.* (1977) sampled micronekton from twelve contiguous depth strata in the upper 1 000 m by IKMT-10 ft equipped with an opening-closing codend. No seasonal change was noted in the pattern of vertical migration and average depth distribution of seven common species, but significant vertical migration was observed in five of the seven common species. The range of diel migration was generally 200 - 400 m. Common migratory species usually occupied depths of 0 - 50 m at night and 300 - 500 m by day. The population of the most common species, *Stenobrachius leucopsarus*, was composed of migratory and non-migratory individuals, and showed two nocturnal peak abundances: at 400 - 600 m and in the upper 100 m. The two groups were similar in size frequency distribution.

Pearcy and Mesecar (1971) and Pearcy (1977) worked on the relationship between sound scattering layers and the vertical distribution of oceanic animals off Oregon. *S. leucopsarus*, together with two species of crustaceans *Euphausia pacifica* and *Sergestes similis*, was caught most often and in the largest numbers from scattering layers, especially in the upper 100 m at night. Small *S. leucopsarus*, having gas-filled swimbladders, were caught in all tows that sampled the DSL (350 - 420 m) during day or night. But the authors stressed the difficulties of predicting the composition of DSLs without more data on scattering properties, abundance and distribution of oceanic species, since close agreement has usually not been found between volume scattering and midwater trawl catches.

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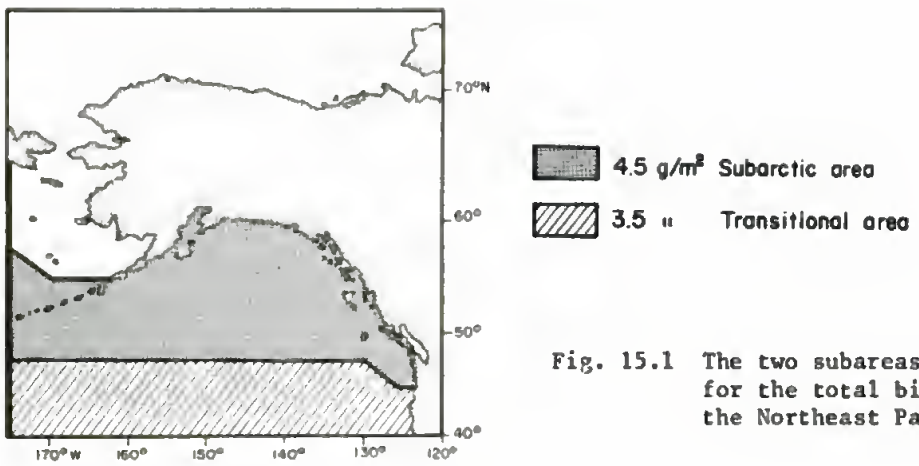

Fig. 15.1 The two subareas and values adopted for the total biomass estimation in the Northeast Pacific.

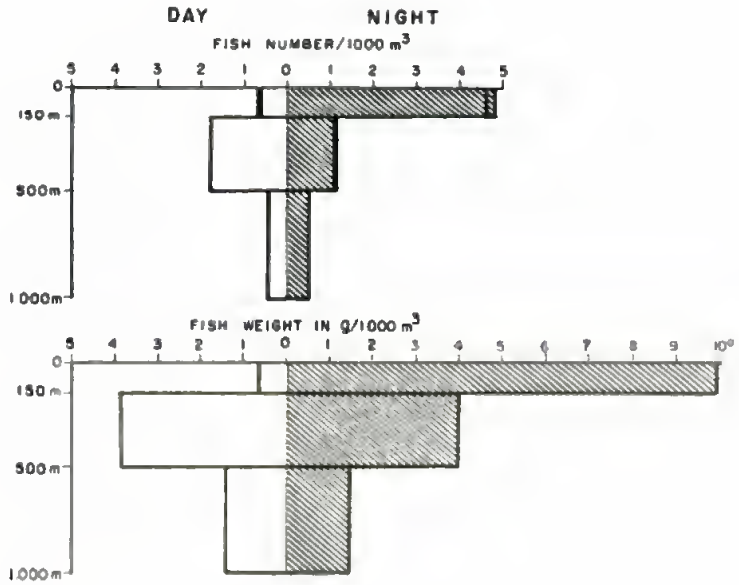

Fig. 15.2 Day-night difference in the vertical distribution of micronektonic fish biomass in the transitional area of the Northeast Pacific (from Pearcy and Laurs, 1966).

Species composition

Pearcy (1977) listed the average daytime catches of mesopelagic fish species in the upper 500 m during the years 1969 - 1973 off Oregon. Table 15.2 from his report shows the average abundance of common mesopelagic fishes in the subarctic and transitional areas, and these figures supported by the results of other investigations (Aron, 1962; Pearcy, 1964; Pearcy and Laurs, 1966, etc.). *Stenobrachius leucopsarus* usually ranks first in abundance. Though their ranks varied, *Diaphus theta, Tarletonbeania crenularis* and *Tactostoma macropus* were common and one of them usually ranked second in abundance. *Protomyctophum crockeri* is a transitional water species and less abundant in subarctic waters. Other common species which are not listed in Table 15.2 include *Ceratoscopelus townsendi, Cyclothone signata, C. pallida* and *C. pseudopallida,* all of which have their distributional centres in the subtropical region to the south.

Life history

The life history of *Stenobrachius leucopsarus* was studied by Smoker and Pearcy (1970). The species spawns from December to March off Oregon. Its early growth is approximately linear with the length of yearling fish averaging 23 mm, of 2-year-olds 41 mm, and of 3-year-olds 59 mm. The inflexion in growth occurs at about 4 years of age. A linear regression of length (mm) on age (months) yields:

$$L_t = 20.78 + 1.59\ t \qquad (r = 0.98)$$

r = Pearsons correlation coefficient

t = age in months

L_t = body length at age t

Based on the otolith analysis of age-groups, the following von Bertalanffy growth equation was also obtained.

$$L_t = 84.96 - 79.32\ e^{-0.34t}$$

These growth and reproduction patterns are similar to those reported for the same species off Monterey Bay, California. The maximum life span by otolith analysis is 8 years, but for the most part reliable readings were limited to fish 5 years old or younger.

16. WESTERN CENTRAL PACIFIC

This area can be divided into three subareas according to the distribution of relative abundance, i.e. the Equatorial Current system area, the Western North and South Pacific Central Water area and the Southeast Asian Seas. Biomass has been measured only with micronekton nets. Acoustic surveys are needed for the slope water species in the Southeast Asian Seas. More taxonomic work is essential for egg and larva surveys, since the Western Central Pacific is one of the richest areas in species diversity of myctophid fishes. At present, identification of most eggs and larvae is impossible due to s lack of studies on their morphology.

Abundance

Gramperin and Rivaton (1966) reported the species composition and relative abundance of mesopelagic fish taken in IKMT-5 ft sampling in the upper 300 m at night along the equator between 160°E and 100°W. They recognized four zones (A - D) based on relative abundance and faunal changes in the group of migratory species, and pointed out the importance of the variable depth of the Cromwell Current along the equator in defining these zones. The oceanic equatorial region of the Western Central Pacific, mostly occupied by zone D in their definition, showed a relatively lower abundance (in numbers caught per tow) than the neighbouring zone C to the east (168°W - 145°W).

Parin *et al.* (1977) measured the total biomass of mesopelagic fishes by IKMT-10 ft sampling down to 1 000 - 1 500 m at 30 stations in the subtropical and tropical western Pacific. Of the 22 values obtained in the Western Central Pacific, 10 are from the Southeast Asian Seas, 7 from the oceanic equatorial water area and 5 from the central water area.

Their values can be converted to g/m^2 in the upper 1 000 m layer by reference to their Figs. 41 and 42, with the results shown below:

	Average g/m^2	Range	No. samples
The Philippine and Indonesian area in the Southeast Asian Seas	4.2	0.6 - 7.7	10
The Equatorial Current area	2.6	1.5 - 4.7	7
The Western North Pacific Central Water area	1.0	0.5 - 1.3	5

ORI-net sampling was done in the 0 - ca. 1 000 m layer at 4 stations scattered in the South China Sea in March 1977 (Kawaguchi, unpublished data). The values were similar from station to station, ranging from 1.4 to 2.1 g/m^2 with an average of 1.8 g/m^2. Based on the conversion ratio 2.6 obtained in the Northwest Pacific (Table 14.4), the averaged ORI-net value 1.80 g/m^2 can be converted to 4.7 g/m^2, the equivalent IKMT-10 ft value. This figure (4.7 g/m^2) in the South China Sea agrees well with the 4.2 g/m^2 measured by Parin *et al.* (1977) in Philippine and Indonesian waters.

Synthesis of abundance estimates

The Western Central Pacific can be divided into three subareas on the basis of the distribution of abundance (Fig. 16.1). These are the Western North or South Pacific Central Water area, the Equatorial Current system area and the Southeast Asian Seas. The Southeast Asian Seas comprise the South China, Sulu, Celebes, Banda and Java Seas and their adjacent waters. Although Parin *et al.* (1977) considered the Banda and Java Seas as falling within the equatorial area, the density of mesopelagic fishes throughout the Southeast Asian Seas is clearly higher than in the more oceanic Equatorial Current system area (Fig. 42 of Parin

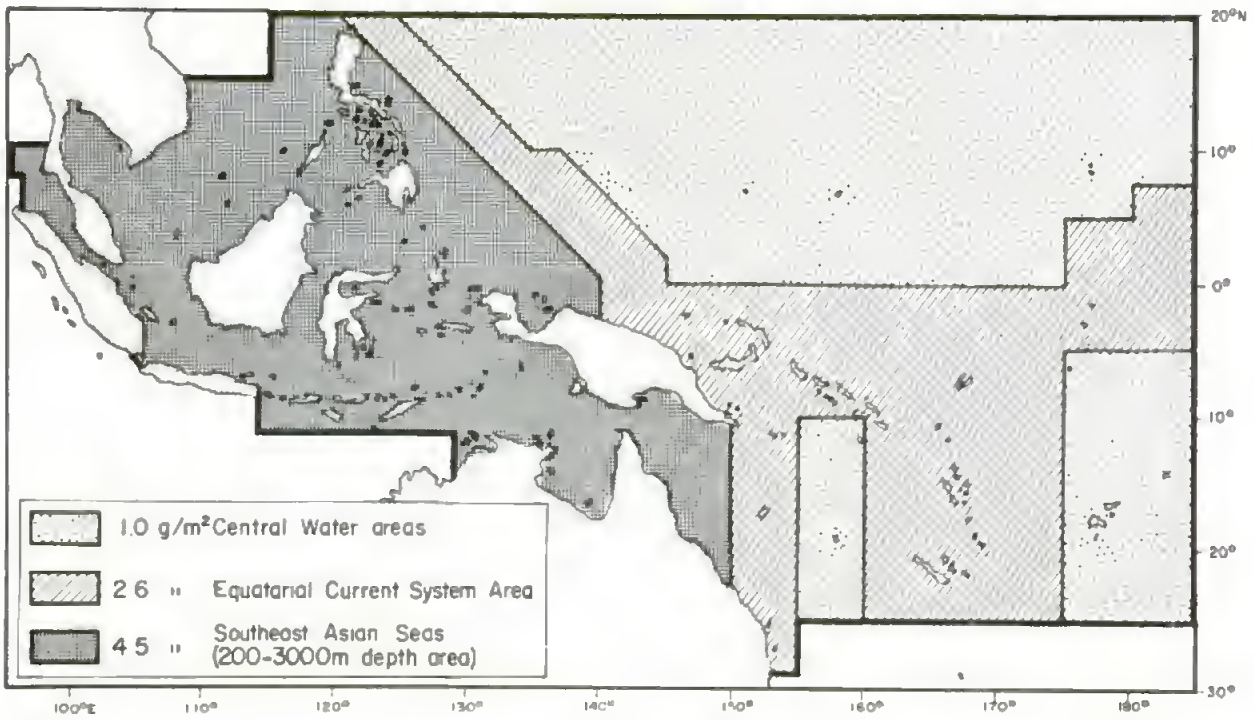

Fig. 16.1 The three subareas and values adopted for the estimation of total micronektonic fish biomass in the Western Central Pacific.

et al., 1977), and these two areas were, therefore, distinguished in the present review. The distributional patterns of primary production and zooplankton abundance also recommend separate treatment of these two areas. Primary production and zooplankton abundance in the South China Sea have been reported to be relatively low compared with other parts of the Southeast Asian Seas, but the density of mesopelagic fish there, measured in March 1977 by Kawaguchi (unpublished), showed no difference from other areas. The South China Sea was therefore not dealt with separately.

For calculating total biomass, the area of the Southeast Asian Seas having depths of 200 - 3 000 m was taken from Moiseev (1971). Estimated densities came mainly from the IKMT-10 ft data of Parin *et al.* (1977) as shown in Table 16.1. Mean density in the Western South Pacific Central Water was assumed equal to that in the Western North Pacific Central Water area (1.0 g/m^2). This value is slightly lower than the 1.3 g/m^2 in the central water area of the Northwest Pacific, but this north-south density gradient seems reasonable in light of the distribution of biomass from the subarctic to the Equatorial Current area. The density in the Southeast Asian Seas is estimated at the same level as in the Kuroshio system area.

The estimated biomass in each subarea is shown in Table 16.1. The estimated total biomass in the Central Western Pacific is 52 x 10^6 tonnes from the IKMT-10 ft data. But it should be noted that the slope water (200 - 1 000 m) of the Southeast Asian Seas is known to be inhabited by the larger myctophid species, especially of the genus *Diaphus*, and their biomass is not included in the estimate owing to their net avoidance (see species composition).

Table 16.1

Estimated total biomass of mesopelagic fish in each subarea of the Western Central Pacific

Subareas	Size of area m^2 x 10^{11}	Density g/m^2 IKMT-10ft (range)	Stock tonnes x 10^6
Southeast Asian Seas	30	4.5 (0.6-7.7)	14
Equatorial Current System area	93	2.6	24
Western North and South Pacific Central Water area	136	1.0 (0.5-1.3)	14
Total			52

Depth distribution

Based on more than 1 500 samples collected by IKMT-10 ft, Legand *et al.* (1972) reported the vertical distributional pattern of micronektonic fishes in the equatorial and tropical regions of the central and western South Pacific, and classified them into two groups, deep non-migrants and midwater migrants. The non-migrants include three species of *Cyclothone* - *C. alba, C. acclinidens* and *C. pallida* - and the hatchet fish, *Sternoptyx diaphana*. Their day and night ranges are between 500 and 800 m. The migrants, mainly myctophids, share their daytime range with non-migrants, but at night rise to the upper layers and even to the surface. The range of vertical migration varies from 200 - 700 m. Usually only a part of the population was observed to ascend at night while the remainder atayed at the usual daytime depth.

Parin *et al.* (1977) sampled five discrete layers down to 1 500 m in the western tropical Pacific by IKMT-10 ft, and observed a bimodal vertical distribution of biomass at night, resulting from the presence of both migratory and non-migratory species or populations. It is remarkable that the biomass in the 1 000 - 1 500 m layer was comparable to that in the upper 200 m at night, and that more than 70% of the biomass was composed of families other than the Gonostomatidae and Myctophidae.

Speciea composition

According to Legand *et al.* (1972) and Parin *et al.* (1977), the following species are supposed to be abundant in the Western Central Pacific:

Gonostomatidae:	*Vinciguerria nimbaria, Gonostoma elongatum, G. atlanticum, Cyclothone alba, C. pseudopallida, C. pallida, C. acclinidens.*
Myctophidae:	*Lobianchia gemellari, Diaphus fulgens, D. splendidus, D. jenseni, D. mollis, D. parri, D. regani, D. malayanus, Lampanyctus niger, L. tenuiformis, L. nobilis, L. alatus, Bolinichthys longipes, Ceratoscopelus warmingi.*
Sternoptychidae:	*Sternoptyx diaphana.*
Chauliodontidae:	*Chauliodus sloani.*

Due to the limitation of sampling techniques and areas, the abundance of surface-migrating species and slope water species is considerably underestimated in the above worka. Therefore the following species should be added, the additional migrants mainly based on Sarenas (1954), Bekker (1964, 1965, 1967) and Kawaguchi *et al.* (1972) and the additional slope water species on Fowler (1934) and Kawaguchi and Shimizu (1978).

Surface migrants:	*Centrobranchus andrae, C. choerocephalus, Hygophum proximum, H. reinhardti, Myctophum spinosum, M. obtusirostrum, M. asperum, M. aurolaternatum.*
Slope water species:	*Diaphus watasei, D. burtoni, D. chrysolynchus, D. suborbitalis, D. umbroculus.*

Life history

No data are available at present.

17. EASTERN CENTRAL PACIFIC

This area includes various water masses and zoogeographical areas. The available information on biomass density is uneven in both quantity and quality from area to area. Five subareas are defined here according to mesopelagic fish abundance, water mass, and faunal zone. All estimates are based on measured or assumed IKMT-10 ft values.

Abundance

Blackburn (1968) studied the distribution of micronektonic fish biomass (ml/10m^3) with a 1.5 m square net in the upper 90 - 95 m layer in the subtropical and tropical eastern Pacific (30°N to 30°S, east of 120°W). The distribution of biomass showed a pattern similar to that of primary production. Fish densities ranged from 3.1 to 81 ml/10^{3}m^3 in the areas where primary production greater than 250 mg C/m^2/day has been observed, but were only 0.3 - 3.0 ml/10^{3}m^3 in the more offshore area where primary production is 100 - 250 mg C/m^2/day. Assuming that the settling volume (ml) is nearly equal to grams wet weight, the above values can be converted to the biomass in the upper 100 m as follows:

productive area	(> 250 mg C/m^2/day)	0.3 - 8.1 g/m^2
offshore area	(100 - 250 mg C/m^2/day)	0.03 - 0.3 g/m^2

The mean values are not reported for these areas, but can be seen from Blackburn's figure to be about 2 - 3 g/m^2 and 0.1 - 0.3 g/m^2 respectively in the 0 - 100 m layer at night. This indicates that densities in the productive area are equal to or greater than those in the upper 0 - 150 m at night in transitional waters of the Northeast Pacific (see Pearcy and Laurs, 1968).

Blackburn *et al.* (1970) analysed seasonal and areal changes in abundance in three large areas of the eastern tropical Pacific, as shown by 248 night samples collected in the upper 200 m layer with a 1.5 m square net during the EASTROPAC expedition, 1967 - 1968. In the western area studied (16°N to 3°20'S, 100°30'W to 121°30'W), sampling was done in seven successive periods of approximately two months each. The seasonal change in fish-cephalopod micronekton abundance (ml/10^{3}m^3) was small, with maximum/minimum ratio less than 2. The maximum and minimum occurred in October-November and April-May, respectively.

Sampling was also done in two different seasons, February-March and August-September, in two neighbouring areas to the east and south. In the eastern area (11°40'N to 15°00'S, 79°45'W to 95°45'W), no significant seasonal change was observed, but significant latitudinal changes were. No seasonal or areal variation was observed in the more offshore southern area (south of 3°20'S and from 10°30'W to 121°30'W).

The distributional pattern of the abundance of the fish-cephalopod micronekton agrees with that of fish only reported by Blackburn (1968):

productive area	(> 250 mg C/m^2/day)	0.4 - 3.3 g/m^2
offshore area	(100-250 mg C/m^2/day)	0.2 - 0.4 g/m^2

Based on this distributional pattern, we defined three subareas: the productive, equatorial and transitional areas (Fig. 17.1).

Off Hawaii, Clarke (1973) made a seasonal study of the size composition, vertical distribution and abundance of myctophid species. Sampling was done in four seasons (September, December, March and June) by IKMT-10 ft and a much larger midwater trawl in the 0 - ca.1000 m layer. The abundance of the dominant nine species was 0.32 g/m^2 in wet weight and 0.55/m^2 in number. He attributed the lowest biomass, observed in June, to the fact that in most species few adults were still alive then while the juveniles of the next generation had not yet recruited to the population, indicating a short life span.

Maynard *et al.* (1975) reported the faunal composition, standing stock and vertical migration of mesopelagic animals off Hawaii, based on ten samples collected by IKMT-10 ft from the 0 - 1 200 m layer in September-October 1972. The catches in day and night sampling were not significantly different in the upper 1 000 m layer. Estimated densities in weight and number are shown in Table 17.1. In total, the density of all species was estimated at 2.57 g/m^2 in wet weight and 5.1/m^2 in number. In light of the study of seasonal variation of myctophid biomass by Clarke (1973), these values obtained in September and October may be assumed to be intermediate between the maximum and minimum.

King and Iversen (1962) reported relative abundance of all micronekton as measured by IKMT-10 ft catches in a wide range of the tropical Pacific (10°N to 10°S, 110°W to 160°W) and the subtropical and subarctic Pacific (150°W to 180°).

Grandperrin and Rivaton (1966) reported faunal changes along the equator from 92°W to 168°W. Hartman and Clarke (1975) also reported s change in the species composition of myctophids along 145°W longitude between 12°N and 3°30'S. These data on relative abundance and faunal changes are also adopted here to define the subareas of different density.

Extensive larval surveys have been carried out in the eastern subtropical and tropical Pacific as part of the CalCOFI and EASTROPAC I and II surveys (Ahlstrom, 1965, 1969, 1971, 1972; Ahlstrom and Counts, 1958). The results have consistently shown the dominance of mesopelagic fish larvae in the oceanic area, although total biomass cannot yet be reliably estimated from these data owing to lack of knowledge on the ecology of the various species, including their fecundity, spawning season etc.

Some qualitative information is available from acoustic surveys. Chapman *et al.* (1975) found a difference in the spectrum of column scattering strength between the north subtropical and the tropical regions of the eastern Pacific. This difference was also observed in volume scattering measurements at 12 kHz (Johnson, 1976). The acoustically detected boundary off the southern end of Baja California coincides with faunal changes in mesopelagic animals, including fishes detected by other means, and is adopted here as the boundary between the tranaitional area and the productive area defined earlier in this section (Fig. 17.1).

Synthesis of abundance estimates

Considering the distributional pattern of abundance together with the zoogeographical zones and major water masses, the Eastern Central Pacific can be divided into five subareas (Fig. 17.1): the transitional area (small transitional area in the South Pacific tentatively being included here), the Eastern North Pacific Central Water area, the Eastern South Pacific Central Water area, the equatorial area and a productive area off Central and South America.

The biomass value of 3.6 g/m^2, obtained in the transitional area of the Northeast Pacific (FAO Fishing area 67), was taken for the transitional zone, since these areas are contiguous and identical.

The Eastern North Pacific Central Water area is rather small and is probably affected by an inflow of biomass from the more productive surrounding areas such as the transitional and equatorial areas. Therefore, its mean biomass density is presumed to be higher than those of the more extensive central water areas in the northwest and southeast Pacific. The density of 2.57 ± 0.81 g/m^2 obtained in September-October 1972 off Hawaii by Maynard *et al.* (1975) is the most reliable value available at present, and is thought to be near the annual mean, since Clarke (1973) found the maximum biomass of nine dominant myctophid species in the same area in December and the minimum in June. But the sampling was done 10 - 25 km off the west coast of Oahu in the Hawaiian Archipelago where the density is thought slightly higher than the average in the open Eastern North Pacific Central Water owing to the effect of the islands. Therefore a lower value, 2.0 g/m^2, was tentatively adopted for the calculation of biomass in the central water of the eastern North Pacific.

Table 17.1

The standing stock of mesopelagic fishes off Hawaii
based on IKMT-10 ft sampling in September-October 1972
(Maynard *et al.*, 1975)

A. Mean biomass, grams wet weight per 100 m^2 ocean surface. Standard deviation in parentheses

Group	0 - 1200 m		Day 0 - 400 m		Night 0 - 400 m	
Myctophidae	65.71	(20.36)	0.19	(0.17)	69.85	(12.26)
Cyclothone	45.91	(11.26)	0.46	(0.75)	1.20	(2.92)
Other						
Gonostomatidae	14.92	(8.48)	0.41	(0.49)	29.24	(25.22)
Sternoptychidae	25.05	(14.02)	0.39	(0.91)	7.45	(2.75)
Other Stomiatoidei	15.56	(12.53)	0.00		13.36	(14.73)
Anguilliformes	48.18	(43.65)	2.40	(3.04)	1.53	(1.63)
Misc. fishes	41.37	(40.16)	2.65	(0.93)	9.46	(6.35)
Caridea	50.49	(21.07)	0.15	(0.28	30.27	(13.11)
Penaeidea	31.59	(10.61)	0.13	(0.10)	22.71	(3.88)
Euphausiacea	18.52	(3.98)	0.86	(0.80)	12.28	(1.57)
Mysidacea	8.80	(9.76)	0.00		4.42	(3.45)
Misc. Crustacea	1.09	(1.92)	0.00		1.09	(0.78)
Cephalopoda	48.71	(47.46)	2.02	(2.02)	13.84	(16.28)
Tunicata	34.07	(42.52)	5.90	(3.50)	21.68	(15.00)
Cnidaria	40.86	(46.86)	10.50	(5.50)	11.34	(12.87)
Misc. invertebrates	3.38	(3.49)	6.61	(2.35)	1.39	(0.33)
Total micronekton	494.20	(99.30)	32.68	(6.58)	251.11	(53.46)
Total fishes	256.70	(81.30)	6.50	(2.99)	132.09	(39.33)
Total Crustacea	110.49	(36.15)	1.14	(1.06)	70.77	(12.30)
Cephalopoda	48.71	(47.46)	2.02	(2.02)	13.84	(16.28)
Other invertebrates	78.31	(53.50)	23.01	(8.34)	34.41	(21.93)
Zooplankton 1/	48.12	(21.64)	15.24	(4.07)	49.20	(12.30)
Zooplankton 2/	471.95	(212.26)	149.45	(39.94)	482.57	(120.91)

1/ Calculated assuming 7.7 m^2 net mouth, full 10-foot IKMT mouth.

2/ Calculated assuming 0.785 m^2 net mouth, cod end mouth area.

Table 17.1 (Contd.)

B. Mean number of organisms per 100 m^2 ocean surface. Standard deviation in parentheses

Group	0 - 1200 m		Day 0 - 400 m		Night 0 - 400 m	
Myctophidae	108.13	(45.71)	1.02	(1.15)	80.72	(22.65)
Cyclothone	308.29	(103.34)	6.07	(8.84)	19.48	(39.01)
Other						
Gonostomatidae	25.77	(3.70)	3.25	(3.84)	22.13	(8.56)
Sternoptychidae	22.97	(5.98)	0.42	(0.78)	4.36	(1.47)
Other Stomiatoidei	3.92	(2.04)	0.00		2.68	(1.70)
Anguilliformes	11.43	(4.46)	2.64	(1.04)	2.96	(2.23)
Misc. fishes	27.49	(7.64)	16.31	(5.68)	21.08	(5.83)
Caridea	40.18	(5.93)	1.70	(2.21)	27.52	(11.18)
Penaeidea	137.90	(34.99)	6.83	(3.74)	132.90	(21.69)
Euphausiacea	97.79	(28.16)	6.79	(5.77)	69.01	(11.50)
Mysidacea	9.89	(3.02)	0.00		8.73	(6.67)
Misc. Crustacea	4.08	(6.72)	0.00		1.88	(1.54)
Cephalopoda	8.44	(2.04)	3.60	(1.98)	5.95	(1.81)
Tunicata	28.05	(14.10)	50.26	(24.73)	25.01	(10.97)
Cnidaria	10.80	(9.41)	11.82	(2.49)	11.47	(8.81)
Misc. invertebrates	52.93	(25.02)	55.55	(7.73)	42.04	(10.03)
Total micronekton	898.07	(149.50)	166.27	(16.45)	477.94	(69.27)
Total fishes	508.00	(133.50)	29.71	(7.48)	153.41	(60.43)
Total Crustacea	289.84	(54.25)	15.32	(4.92)	240.04	(13.91)
Cepholopoda	8.44	(2.04)	3.60	(1.98)	5.95	(1.81)
Other invertebrates	91.78	(25.22)	117.63	(19.26)	78.52	(22.71)
No. organisms caught	12 037		1 576		5 136	
No. tows	9		6		7	

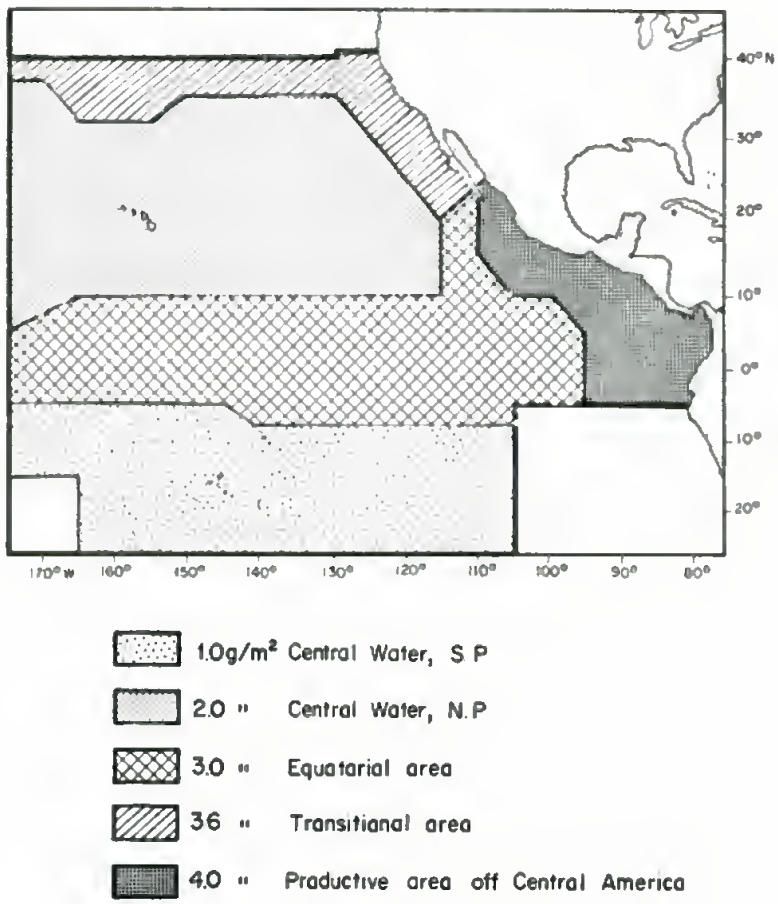

Fig. 17.1 The five subareas and values used for the total biomass estimation of micronektonic fish in the Eastern Central Pacific.

No measured value for the central waters in the eastern South Pacific is available at present, so the lower value 1.0 g/m^2 from the southern part of the Western North Pacific Central Water area was adopted for making a conservative estimate.

In the productive area east of the equatorial area, data from deep tows is lacking, but the value of 4 g/m^2 is considered reasonable because densities of 2 - 3 g/m^2 have been observed in the uppermost 100 m at night.

In the equatorial region, 3.0 g/m^2 was considered reasonable on the basis of the extensive data on relative abundance from IKMT-10 ft catches (King and Iversen, 1962), primary productivity and zooplankton volumes, although a reliable value is not yet available for this area.

The biomass in each subarea is shown in Table 17.2. The total biomass in FAO Fishing area 77 was estimated to be 129 x 10^6 tonnes, with species composition and productivity probably varying considerably from area to area.

The need for more reliable biomass data on the equatorial area, the central water in the South Pacific and the productive area should be stressed again.

Table 17.2

Estimated total biomass of the mesopelagic fish in the Eastern Central Pacific based on measured or assumed biomass densities by IKMT-10 ft

Subareas	Size of area x 10^{11} m^2	Biomass g/m^2	Total biomass x 10^6 tonnes
Transitional area	48	3.6	17
Eastern North Pacific Central Water area	158	2.0	32
Eastern South Pacific Central Water area	143	1.0	14
Equatorial area	162	3.0	49
Productive area off Central America	43	4.0	17
Total			129

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Depth distribution

Paxton (1967a) analysed the distributional pattern of the lanternfishes of the San Pedro Basin, California by successive IKMT-10 ft hauls to various depths. By day all the fifteen species recorded were taken below 350 m, with the centre of concentration between 450 and 700 m. Five species showed peak abundance below 650 m and ten species above 650 m during the day. At night, four shallow species ascend the upper 10 m, five to 50 m, and one to only 150 m. Of the five deep species, two were non-migrants and three migrated to 50 m depth. He pointed out temperature and light as the most important determinants of vertical distribution, and suggested that the shallow thermocline might set the upper limits of vertical migration of some species.

Barham (1966, 1970) observed myctophid fishes, including *Triphotrus mexicanus* and *Stenobrachius leucopsarus*, off southern California from deep submersible vehicles. He reported a dense concentration in the upper 100 m at night and in the 300 - 400 m layer during the day, and related it to the deep scattering layers.

Maynard *et al.* (1975) studied the faunal composition, standing stock and diel vertical migration of mesopelagic micronekton in Hawaiian waters by 9 deep-oblique tows (0 - 1 200 m) and a 24-hour series of 14 consecutive shallow-oblique tows (0 - 400 m). Of the total fish biomass of 256.7 g/100 m^2 ocean surface in the 0 - 1 200 m layer, 132.1 g/100 m^2 migrated up to the upper 400 m. About 50% of the migratory biomass was composed of myctophids and the other half mainly of gonostomatids, sternoptychids and other stomiatoids.

In the Hawaiian waters, Clarke (1973) reported the vertical distribution of 47 myctophid species. Most species showed ontogenetic differences in vertical distribution and migration, with the smaller fish tending to occur shallower than the adults. Large fractions of the populations of three species, *Notolychnus valdiviae*, *Lampanyctus niger* and *Triphoturus nigrescens*, appeared not to migrate in certain seasons.

Species composition

Berry and Perkins (1966) surveyed the mesopelagic fishes of the California Current area (20°N - 40°N), collecting 198 samples between May 1961 and March 1963. More than 189 species and about 52 000 specimens were taken. The greatest number of species in a single family was 40 in the Myctophidae. The most common species in the 198 samples are listed below with the number of positive stations in parentheses.

Myctophidae:

Triphoturus mexicanus	76
Protomyotophum crockeri	66
Ceratoscopelus townsendi	66
Lampanyctus ritteri	63
Diaphus theta	61
Symbolophorus californiense	55
Stenobrachius leucopsarus	54
Tarletonbeania crenularis	45

Gonostomatidae:

Vinciguerria lucetia	25
Cyclothone signata	64
C. acclinidens	49
Danophos oculatus	47

Sternoptychidae

Argyropelecus hawaiensis	54
A. pacificus	49
A. intermedius	45

The most abundant mesopelagic species in a single tow was *T. mexicanus*, with about 3 000 specimens taken at one station and 1 857 at another. Other large single collections were of *C. townsendi* (944), *S. leucopsarus* (735) and *V. lucetia* (537). These results in the transitional area of the Eastern Central Pacific are believed to be reliable, since the sampling coverage was wide in both area and season. A similar species composition has been reported by Paxton (1967a). It is notable that the species composition varies from north to south, with the subarctic species being gradually replaced by the transitional, central water and equatorial species (see Table 15.2).

Off Hawaii, Clarke (1973, 1974) reported some aspects of the ecology of myctophids and stomiatoids based on the four series of samples collected quarterly from September 1970 to June 1971 in the upper 1 000 m. The dominant species were as below, the figures to the right showing number of specimens collected and their size range in mm.

Myctophidae

Ceratoscopelus warmingi	3 911	11 - 79
Lampanyctus steinbecki	2 362	14 - 56
Triphoturus nigrescens	2 120	9 - 38
Lampanyctus niger	1 946	12 - 135
Bolinichthys longipes	1 458	11 - 56
Notolychnus valdiviae	1 267	9 - 25
Benthosema suborbitale	1 157	9 - 38
Diaphus schmidti	823	9 - 47
Hygophum proximum	696	12 - 51
H. reinhardti	413	12 - 48

Gonostomatidae

Vinciguerria nimbaria	2 927	8 - 49
Cyclothone alba	-	-
C. pseudopallida	-	-
C. pallida	-	-
C. acclinidence	-	-
Gonostoma atlanticum	680	10 - 66
G. elongatum	1 346	10 - 218
Valenciennellus tripunctulatus	600	10 - 32

The species of the genus *Cyclothone* in the above list were added on the basis of reports by Makhacheva (1964). This genus was not dealt with by Clarke (1974).

In the equatorial region, Hartman and Clarke (1975) analysed the distributional pattern of myctophids collected in the upper 50 - 75 m at night along 145°W longitude between 12°N and 3°30'S and identified three faunal groups. The first group was distributed across the entire transect, being most abundant at or just north of the equator, and included *H. proximum*, *Symbolophorus evermanni*, *T. nigrescens*, *C. warmingi* and *B. longipes*. The second group occurred only in the North Equatorial Current or the Counter Current, and included *Diogenichthys laternatus*, *Diaphus garmani*, *Lampanyctus nobilis* and *L. omostigma*. The third group occurred only in the productive area at or just north of equator, and included *Diaphus malayanus*, *D. signatus*, *Lampanyctus bubbsi*.

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Grandperrin and Rivaton (1966) pointed out four faunal zones along the equator between 92°W and 162°E, based on the analysis of 24 IKMT-5 ft samples collected at night in the upper 300 m. Each zone was marked at the time of the cruise by an 'endemic' fauna that could be related to the variable depth of the Cromwell Current along the equator. Three of the four zones fall within the Eastern Central Pacific.

All the findings mentioned above show that the Eastern Ce..tral Pacific takes in several different zoogeographical areas which may be further divided into subareas. Species composition is believed to vary in each subarea.

Life history

Stenobrachius leucopsarus shows the same growth and reproduction patterns in Monterey Bay, California, as it does off Oregon, although the spawning season is about 2 - 3 months delayed in Monterey Bay (Fast, 1960; Smoker and Pearcy, 1970).

Clarke (1973) studied some aspects of the ecology of 47 myctophid species off Hawaii, and estimated the spawning season of 23 species and sizes at maturity for 33 species. Most myctophids studied were believed to have a one-year life cycle, so in many species the population would be almost totally replaced with each new generation. A similar life history pattern seems to be common in tropical species, especially the species less than about 50 mm as adults.

18. SOUTHEAST PACIFIC

Information on abundance and depth distribution is limited in this region. Therefore, biomass densities were mostly inferred by analogy from values measured in similar areas elsewhere.

This area was divided into four subareas: the upwelling area off Peru and Chile, the Eastern South Pscific Central Water area, the subantarctic area, and the transitional areas.

Abundance

Blackburn (1968) reported the abundance of micronektonic fish in the upper 95 m at night as shown by 1.5 m square net samples. The area surveyed covers a wide area from the coast to as far westward as 95°W between 5°S and 25°S, providing useful information for the definition of subareas.

Cradock and Mead (1970) reported the inshore-offshore variation in abundance of midwater fish (ml/hr collected by the IKMT-10 ft) along 34°S latitude between 72°W and 92°W. The higher biomass values, 100 - 600 ml/hr, were obtained in the inshore area east of 75°W and the values for the more offshore areas were below 100 ml/hr and not highly variable.

The results of larval surveys indicate that the larvae of one genus of the Gonostomatidae occur in greater total abundance than those of the anchoveta (pers. com. Dr. R. Jordan, IMARPE, Peru).

Synthesis of abundance species

Based on the limited data available and the distribution of primary production and zooplankton biomass, this area was divided into four subareas as shown in Fig. 18.1. Mean density in the upwelling area off Peru was assumed to be the same as in the highly productive area off Central America in the neighbouring Eastern Central Pacific. Density values for the transitional, subantarctic and central water areas were inferred by analogy from the values in other areas that are similar to these subareas in terms of primary production and zooplankton abundance.

The biomass estimated for each subarea is presented in Table 18.1, with a total of 52 x 10^6 tonnes in the entire area. Estimates based on reliable field data are badly needed for the Southeast Pacific, especially the upwelling and subantarctic areas.

Table 18.1

Estimated total biomass of mesopelagic fishes
in each subarea of the Southeast Pacific

Subareas	Size of subarea $m^2 \times 10^{11}$	Density g/m^2	Stock tonnes x 10^6
Upwelling area off Peru	11	4.0	4
Eastern South Pacific Central Water	49	1.3	6
Transitional area	86	3.6	31
Subantarctic area	23	4.5	10
Total			51

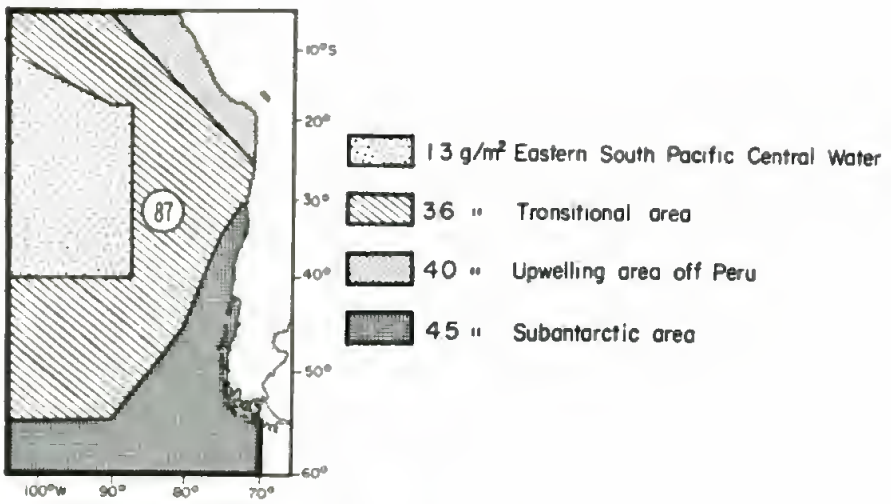

Fig. 18.1 The four subareas and values adopted for the total biomass estimation of micronektonic fish biomass in the Southeast Pacific

Depth distribution

No quantitative information is available at present.

Bussing (1965) reported that fewer individuals and species were taken in the deeper hauls than in hauls of less than 2 000 m in the Southeast Pacific. It is remarkable that large numbers of individuals and species of fishes were collected in the oxygen minimum zone (0.2 - 0.5 ml/ℓ) between 50 and 800 m and the greatest number of specimens (2 765) in a single haul was presumably captured at 680 m which coincides with the oxygen minimum layer at that locality.

Species composition

Extensive faunal studies of mesopelagic fishes were done by Bussing (1965) and Parin *et al.* (1973) in the eastern South Pacific. According to their findings, the area is inhabited by four groups of species, i.e. the equatorial water species, the central water species, the subantarctic water species and the cosmopolitan species. The area off Peru and Chile is a zone of zoogeographic transition where the fishes of all four groups occur. The common myctophid and gonostomatid species in their samples are as follows:

Gonostomatidae: *Vinciguerria lucetia, Cyclothone signatha, C. acclinidens.*

Myctophidae: *Hygophum reinhardti, Diogenichthys laternatus, Symbolophorus boops, S. evermanni, Myctophum aurolaternatum, M. nitidulum, Gonichthys tenuiculus, Notolychnus valdiviae, Triphoturus mexicanus, Lampanyctus achirus, L. omostigma, L. parvicauda.*

Life history

No information is available.

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19. SOUTHWEST PACIFIC

This area wss divided into three subareas: the central, transitional and subantarctic areas (Fig. 19.1). The subareas were defined on the basis of the distribution of primary production, zooplankton abundance and water masses, and mesopelagic fish densities were estimated on the basis of the observed relationship between environmental conditions and density in other areas. Future estimates based on measured biomass density may well result in appreciable corrections in this area.

Abundance

For the density in the eastern South Pacific Central Water area we adopted the value of 1.3 g/m^2 obtained in the northern part of the Western North Pacific Central Water area, considering the rather high biomass density in the neighbouring transitional and subantarctic areas. For convenience, the small productive area off northern New Zealand is included in the subantarctic area. The value of 4.5 g/m^2 for the subantarctic was set at the same level as in the eastern subarctic, and the value of 3.6 g/m^2 for the transitional area is that measured in the transitional area in the Northeast Pacific. The estimated biomass in each subarea is shown in Table 19.1. A total of 101 x 10^6 tonnes was estimated in this area.

According to Robertson (1977), the stock of *Lampanyctodes hectoris*, the only myctophid species commercially fished off southwest Africa, seems considerable off New Zealand. Future abundance surveys of this species should be carried out.

Table 19.1

Estimated total biomass of mesopelagic fishes
in each subarea of the Southwest Pacific

Subareas	Size of subarea m^2 x 10^{11}	Density g/m^2	Stock tonnes x 10^6
Eastern South Pacific Central Water area	98	1.3	13
Transitional area	147	3.6	53
Subantarctic area	78	4.5	35
Total			101

Depth distribution

No reliable information is available, but the vertical distributional pattern of biomass is probably similar to that in similar areas elsewhere, since the species composition partly overlaps that of neighbouring areas where the pattern is well known, for both migratory and non-migratory species.

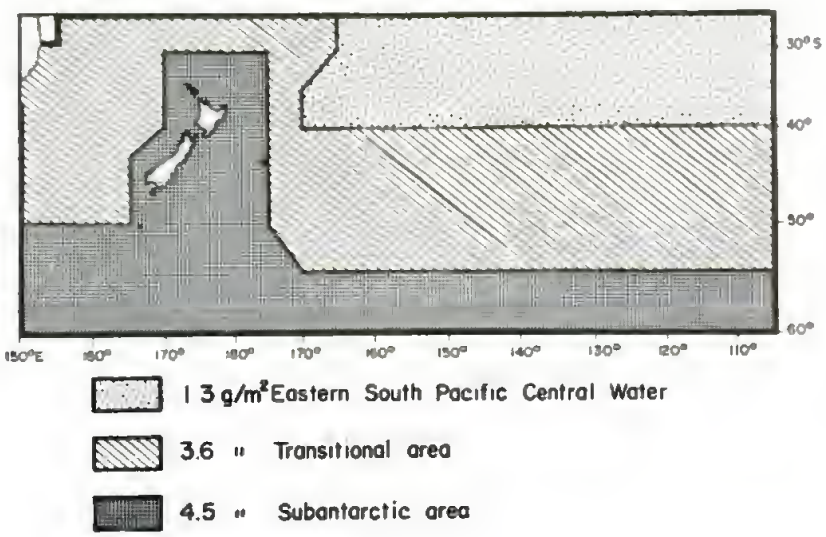

Fig. 19.1 The three subareas and values used for the total biomass estimation in the Southwest Pacific.

Species composition

Quantitative studies on the species composition have not yet been done in the Southwest Pacific, but according to the results of zoogeographical surveys (Andriyashev, 1962; Bekker, 1965; Nafpaktitis and Paxton, 1968; Nafpaktitis and Nafpaktitis, 1969: Gorbunova, 1972; Mukhacheva, 1972, 1974; Wisner, 1976, etc.), the following species are believed to be common in the area.

Myctophidae: *Protomyctophum andersoni, P. normani, P. bolini, P. subparallelum, Electrona carlsbergi, E. subaepera, Diogenichthys atlanticus, Hygophum hygomi, H. reinhardti, H. hanseni, Symbolophorus boops, Gonichthys barnesi, Centrobranchus choerocephalus, Diaphus hudsoni, Lampadena speculigera, L. dea, L. notialis, L. chavesi, Lampanyctus intricariue, L. australis, Lampanyctodes hectoris, Ceratoscopelus warmingi, Gymnoscopelus piabilis.*

Gonostomatidae: *Cyclothone pseudopallida, C. pallida, C. microdon, Gonoetoma bathyphilum, G. longipinnis, Vinciguerria attenuata.*

Life history

The eggs of *L. hectoris*, reported from off New Zealand, are the first myctophid eggs ever identified to species (Robertson, 1977). Future life history studies of this species are expected, since at present *L. hectoris* is the only exploited species among the mesopelagic fishes. Life history studies of other species are lacking in this area.

20. THE ANTARCTIC

The Antarctic as defined here is the area south of the Antarctic Convergence, roughly corresponding to 50°S in most of the Atlantic and Indian Ocean sectors and to 60°S in the Pacific sector.

The Antarctic region is one of the least known as far as mesopelagic fish are concerned, since scientific work there has been seriously restricted by its remote location and severe sea conditions, especially in winter. In view of the lack of data and the absence of any well surveyed area analogous to the Antarctic, no estimation of stock size was attempted for this review.

Only a brief description of the Antarctic mesopelsgic fish fauna will be given here, based mainly on Andriyashev (1962). The waters around Antarctica are inhabited by the pelagic fishes belonging to at least a score of families including the Myctophidae and Gonostomatidae. Other major families are the Bathylagidae, Paralepididae, Macruridae, Scopelarchidae, Melamphaeidae, Trichiuridae, Notothenidae and Chaenichthyidae. In the northern area near the Antarctic Convergence, there occur fishes of the families Sternoptychidae, Astronestidae, Idiacanthidae, Stomiatidae, Notosudidae, Anotopteridae, Moridae, Oreosomatidae and Cerathidae, which are common also in the subantarctic zone between the Antarctic Convergence and the Subtropical Convergence. But it should be noted that the number of meso- and bathypelagic families and their species diversity increase rapidly north of the Antarctic Convergence.

In regard to the fishes of the Myctophidae and Gonostomatidae, the former exceed the latter in the species diversity and probably in biomass. The main Antarctic gonostomatids hitherto reported are the non-migratory species of the genus *Cyclothone (C. microdon* and *C. pseudopallida)*. Therefore, their fishery potential seems low. The common myctophid species are listed below. The Antarctic myctophid fauna is marked by the three diverse genera *Protomyctophum, Electrona* and *Gymnoscopelus*.

Myctophidae: *Protomyctophum andersoni, P. bolini, Electrona antarctica, E. carlsbergi, Gymnoscopelus braueri, G. nicholsi, G. piabilis.*

Of these, *E. antarctica* and *G. braueri* are thought to be the most abundant, based on their frequency of occurrence in samples on zoogeographical surveys. It is noteworthy that most of these species have a circumpolar distribution around the Antarctic continent.

No information on life history is available except Yefremenko's (1977) report of myctophid eggs at the cleavage stage in depths of 200 - 500 m in the Scotia Sea (Ca. 55°S, ca. 40°W) in the Atlantic sector.

There remains much to be learned about the mesopelagic fishes of the Antarctic region. International cooperative surveys such as BIOMASS should produce extremely reliable information.

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21. DISCUSSION OF FISHERY POTENTIAL

21.1 Summary of abundance information

Some of the information on density and total biomass of mesopelagic fish is summarized in Table 21.1. Although the data are sparse, and most of the gears used to obtain the available information obviously underestimate the biomass present, there is little doubt that the density of mesopelagic fish in offshore areas is generally low, and probably mostly below 10 g/m^2. The density may, however, be considerably higher along continental shelves. In the Arabian Sea there is good evidence of very large stocks of mesopelagic fish, and there are also indications of high densities off West Africa and possibly on both sides of South America. But there are also highly productive coastal areas where the densities of mesopelagic fish seem to be quite modest, e.g. off Mozambique and off the Seychelles.

Atlantic Ocean

In the Atlantic there are several interesting areas. Off western and southwestern Africa there are indications of high densities of mesopelagic fish, but there is no reliable data on the size of these neritic stocks. The fishery off southwestern Africa seems to indicate that there is a seasonal variation in the abundance of *Lampanyctodes hectoris* near shore, or at least in availability to the fishing gear. There also seem to be large fluctuations from year to year.

Off other parts of West Africa there is no information on seasonal or annual variation in the density of mesopelagic fishes.

Off southern Norway and west of Great Britain mesopelagic fish seem to occur in fairly high densities, and they sometimes form aggregations vulnerable to fishing gears. In this area too, the data on natural fluctuations are sparse.

Off central parts of South America there are indications of large mesopelagic fish shoals, but more investigations are needed before any conclusions can be reached.

Indian Ocean

The Arabian Sea seems to hold the largest stock of mesopelagic fish known so far. Stock size estimates for the eastern and northern part of the area have been obtained over a period of several years, and 5 estimates for the area ranged between 60 and 150 million tonnes. Other estimates covering only part of the area suggest a still wider range of variation. It is not known how much of the observed variation is caused by sampling error and how much by real fluctuation in stock size.

The stock of slope water species seems considerable in the Bay of Bengal and off the southern coast of Australia, although there remains much to be surveyed.

Pacific Ocean

Most of the FAO Fishing Areas in the Pacific include various water masses and zoogeographical zones. In this review, each area has been subdivided in accordance with relative densities (Sections 14 to 19). All of the subareas are shown in Fig. 21.1 with the density value (g wet weight/m^2) adopted for estimating total biomass.

In the North Pacific, the distributional pattern of mesopelagic fish, as so far measured, conforms with the distribution of the major water masses, primary production and zooplankton abundance. Faunal change of mesopelagic species also corresponds to this pattern. These relationships were assumed to exist, and were used for estimating biomass in

Table 21.1

Summary of mesopelagic fish densities and stock sizes

Area	Main investig.[1/]	Dominant species	Density g/m^2	Biomass tonnes x 10^6
N.E. Atlantic				
Offshore N of 60°N	MN	*Benthosema glaciale*	0.1 - 2	2
Offshore S of 60°N	MN	*Benthosema glaciale*	0.5 - 2	10
Neritic W of G.Britain and Norway	ANR	*Maurolicus muelleri*	10 - 35	3
	ELS		12	
			Total	15
N.W. Atlantic				
N of 60°N	MN	*Benthosema glaciale*	5 - 8	3
	AR		0.1 - 4.7	
S of 60°N	MN	*Ceratoscopelus maderensis* *Benthosema glaciale*	0.1 - 1.7	5
Neritic S of Newfoundland	DO	*Ceratoscopelus maderensis* *Benthosema glaciale*	10 - 60	7
			Total	15
E.C. Atlantic				
Offshore waters	MN	*Cyclothone spp.* *Argyropelecus hemigymnus*	4 - 6	67
Mauritanian upwelling	ANR/CT	*Diaphus dumerili*	15 (-60)	10
			Total	77
W.C. Atlantic				
Gulf of Mexico	MN	*Notolychnus valdiviae*	0.1	1
Caribbean	MN	*Diaphus dumerili*	0.1	2
Oceanic Areas	MN	(*Diogenichthys atlanticus*)	0.1 - 0.2	17
	AR	(*Ceratoscopelus warmingi*)	0.2 - 1	
		(*Lepidophanes guentheri*)		
			Total	20
S.E. Atlantic				
Coastal zone	MN	*Lampanyctodes hectoris*	3 ?	2 ?
Offshore areas	MN	?	1	16
	CT		1.2	
			Total	18

[1/] See list of abbreviations at end of table.

Table 21.1 (Contd.)

Area	Main investig.[1/]	Dominant species	Density g/m^2	Biomass tonnes x 10^6
Northeast Pacific				
Subarctic area	MN	*Stenobrachius leucopsarus* *Diaphus theta* *Tarletonbeania crenuralis*	4.5	15
Transitional area	MN	*Stenobrachius leucopsarus* *Diaphus theta* *Protomyctophum crockeri*	3.6	12
			Total	27
Western Central Pacific				
Southeast Asian Seas	MN	*Diaphus garmani* *D. regani* *D. suborbitalis*	4.5	14
Equatorial current system area	MN	*Diaphus garmani*	2.6	24
Western North and South Pacific Central Water areas	MN	*Diaphus malayanus*	1.0	14
			Total	52
Eastern Central Pacific				
Transitional area	MN	*Triphoturus mexicanus* *Protomyctophum crockeri* *Ceratoscopelus townsendi* *Vinciguerria lucetia*	3.6	17
Eastern North Pacific Central Water area	MN	*Ceratoscopelus warmingi* *Lampanyctus steinbecki* *Triphoturus nigrescens* *Vinciguerria nimbaria*	2.0	32
Eastern South Pacific Central Water area	X		1.0	14
Equatorial area	X	*Hygophum proximum* *Diaphus garmani* *Diogenichthys laternatus*	3.0	49
Productive area off Central America	X		4.0	17
			Total	129

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Table 21.1 (Contd.)

Area	Main investig.[1/]	Dominant species	Density g/m^2	Biomass tonnes x 10^6
S.W. Atlantic				
Coastal zone	CT	*Diaphus dumerili*	high ?	2
Offshore areas	MN		3	39
	CT		0.5	
	AR		0.3 - 1.8	
			Total	41
Mediterranean				
	MN	*Cyclothone braueri*	0.1 - 1	2
	AR		2	
			Total	2
W. Indian Ocean				
Arabian Sea West	ANR/CT	*Benthosema pterotum*	8 - 220	100
" " East	ELS	*Benthosema pterotum*	30	15
Off Mozambique	ANR/CT	*Diaphus spp.*	1 - 30	2
Oceanic areas	MN	Various	0.5	140
			Total	257
Eastern Indian Ocean				
Subarea I	MN	*Diaphus luetkeni*	4.7	16
Subarea II	MN	*D. splendidus*	3.8	29
Subarea III	MN		3.1	38
Subarea IV	MN		1.8	11
			Total	94
Northwest Pacific				
Subarctic area	MN	*Stenobrachius nannochir*		
		S. leucopsarus	6.5	16
		Diaphus theta		
Kuroshio system area	MN	*Diogenichthys atlanticus*		
		Benthosema suborbitale	5.2	21
		Diaphus kuroshio		
		Gonostoma gracile		
		Cyclone atraria		
		Vinciguerria nimbaria		

Table 21.1 (Contd.)

Area	Main investig. 1/	Dominant species	Density g/m^2	Biomass tonnes x 10^6
Northwest Pacific (Contd.)				
Western North Pacific Central Water area	MN	*Cyclothone atraria*	1.3	12
		Gonostoma gracile		
		Diogenichthys atlanticus		
		Benthosema suborbitale		
			Total	49
Southeast Pacific				
Upwelling area off Peru	X		4.0	4
Transitional area	X		3.6	31
Eastern South Pacific Central Water	X		1.3	6
Subantarctic area	X		4.5	10
			Total	51
Southwest Pacific				
Eastern South Pacific Central Water	X		1.3	13
Transitional area	X		3.6	53
Subantarctic area	X		4.5	35
			Total	101

Abbreviations

MN	Micronekton nets
CT	Commercial trawls
ELS	Egg and larva surveys
ANR	Acoustics, non-resonant frequencies
AR	Acoustics, resonant frequencies
DO	Direct observations from submissibles
X	No quantitative field data; densities estimated by analogy with similar areas elsewhere

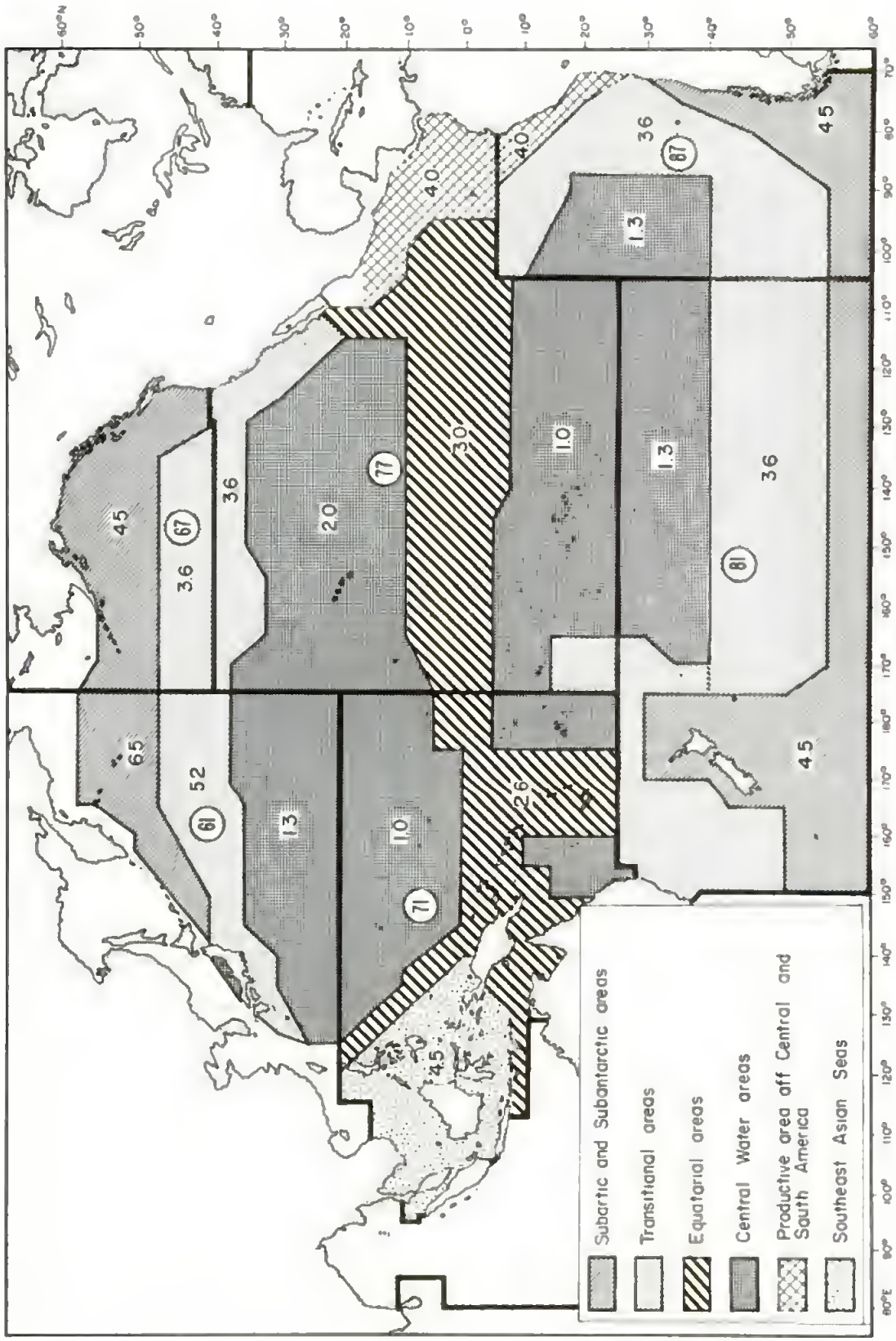

Fig. 21.1 Shows the estimated density values (g/wet weight/m^2) for the FAO fishing areas in the Pacific Ocean

the South Pacific for which no reliable data are available at present. Although no zoogeographical data collected so far have contradicted these relationships, it should be stressed that these estimates can only be tentative until reliable direct measurements are made.

All of the adopted density values are based on micronekton nets of various kinds, converted to equivalent IKMT-10 ft values, with the exception of IKMT-6 ft values in the subarctic eastern Pacific. Acoustic and egg and larva surveys are still inadequate for estimating biomass in the Pacific.

The most promising areas for future surveys, from the fisheries standpoint, can be identified as the productive area off Central and South America, the Southeast Asian Seas, and the subarctic and subantarctic areas, mainly on the basis of high density in those areas (Fig. 21.1).

In the subarctic area, a total stock of 31×10^6 tonnes was estimated. Most of the stock is composed of oceanic species, some of which possibly form localized dense patches. Therefore, future study should be directed to the schooling behaviour or patchy distribution of the dominant species. Acoustic and egg and larva surveys may be also promising because of the rather simple, abundant fauna in this region. In the subantarctic area the present estimate should be interpreted as tentative; future estimates based on direct measurements may well result in large corrections.

The Southeast Asian Seas, including the South China, Sulu, Celebes and Banda Seas, show high biomass densities, comparable to the subarctic region, and total biomass was estimated as 14×10^6 tonnes. This area is also rich in the larger myctophid species endemic to the slope waters, since the continental and insular slopes are well developed here (Table 21.3). But most of the stock of large myctophids is not included in the present estimate, mainly owing to their effective net avoidance (see Section 16). Acoustic surveys are needed to estimate the abundance of these large myctophids.

In the equatorial area off the coasts of Central and South America, the total biomass was estimated as 21×10^6 tonnes, but scientific work is still insufficient to estimate the total biomass reliably. Future abundance surveys should take into account the effects of upwelling and the oxygen-minimum layer on the distribution of mesopelagic fishes.

Among the other areas not yet mentioned, the transitional zone or the Kuroshio area north of its axis is considerably productive, inhabited by endemic species and a promising area for future study.

Finally, the total biomass estimated in this review should be interpreted only as a value based on the data now available. Future refinements of estimates may well result in substantial changes in several cases. But we believe that the true total biomass is within three times the biomass estimated by the IKMT-10 ft data in the oceanic area.

21.2 Potential yield

A simple, approximate estimate of the maximum annual yield of an unfished population can be derived from the equation $Y_{max} = \frac{1}{2} MB_o$ where M is natural mortality and B_o biomass of the unfished stock (Gulland, 1971; Clark, 1978).

For most tropical mesopelagic fish the instantaneous mortality rate is supposed to be higher than 2. Therefore, the annual yield can, according to the formula, be higher than the mean standing stock. For temperate species the few estimates available suggest mortality rates between 0.7 and 2, and potential yield may therefore be about half the amount of the standing stock.

These estimates must, however, be treated very carefully. It is not known how mesopelagic fish species will react to exploitation, but as they generally have a low fecundity there may be a closer correlation between parent stock size and subsequent recruitment than

in most other fish stocks. The low fecundity may make them vulnerable to reproductive failure which may cause the stocks to collapse. Therefore, it is of vital importance that any fishing for these species be carefully monitored to study any variation in growth, natural mortality and recruitment.

21.3 Species of potential commercial interest

In Table 21.1 we listed the dominant species in various regions mainly based on the micronekton net catches. But the species listed do not always correspond to the species of potential commercial interest due to the limited catching ability of micronekton nets, especially with respect to large or surface migrating myctophid fishes. To offset these shortcomings, the species of potential commercial interest will be discussed here in relation to their distributional pattern, regardless of their frequency in micronekton net catches.

In considering the possibility of harvesting mesopelagic species, several factors must be taken into account. One is behaviour in relation to fishing techniques, e.g. schooling behaviour, diel vertical migration, attraction to light. Other factors are related to fishery planning and management such as potential yield and its variability. Finally, ways of processing and marketing the catch are still to be developed.

The vertical distributional pattern is a very important factor for a potential fishery. According to their vertical migrations, mesopelagic species can be broadly classified as surface migrants, midwater migrants and non-migrants.

Surface migrants: Most of the myctophid species of the genera *Loweina, Tarletonbeania, Gonichthys, Centrobranchus, Hygophum, Symbolophorus* and *Myctophum* are known to concentrate in the uppermost 10 m or less at sunset and return to the upper mesopelagic zone below 200 m at dawn. Species which may be considered as interesting members of this group are listed in Table 21.2. At night they are collected in considerable quantities by surface tows made from the side of a ship but they are rarely collected in tows made from the stern due to scattering of fish in the ship's path. They are also lured by a floating ship's lights or fish-luring lights and often dipnetted. During the daytime they are difficult to catch with small trawls such as micronekton nets, probably because of visual net avoidance in the upper mesopelagic zone. These traits suggest that the biomass of these species has probably been greatly underestimated in surveys done with micronekton nets.

Their biomass is also difficult to estimate by acoustic methods as they are above the range of hull-mounted echosounders during the nighttime. As this group usually has well-developed gas-filled swimbladders, they form a good acoustic target during the daytime. Surveys by this method seem promising.

Midwater migrants: Species of this group do not occur at the surface at night, but they form dense concentrations within the upper 100 m. The group can be divided into oceanic and slope water species based on their horizontal distribution.

At present the slope water species are the most promising group since they are vulnerable to existing fishing techniques or slight modifications of them. During the daytime some of them stay just off the bottom (benthopelagic layer) over insular or continental shelves and slopes, and can be caught in bottom trawls. At night they can be caught by commercial midwater trawls when they migrate to the upper 100 m. The only existing myctophid fishery, in South Africa, catches a species of this group (*Lampanyctus hectoris*). The important slope water species to be surveyed are listed in Table 21.3.

In regard to oceanic species, the subarctic, antarctic and transitional areas are thought to be more promising than the tropical zone because they have simpler faunas and higher densities. The interesting species are *Benthosema glaciale* in the North Atlantic and *Stenobrachius leucopsarus* and *Diaphus theta* in the North Pacific. The antarctic myctophids, *Electrona antarctica* and *Gymnoscopelus braueri* are also of great interest.

Table 21.2

Common surface-migrating myctophid species in the Atlantic, Indian, Pacific and Antarctic Oceans

Species	Atlantic Ocean	Indian Ocean	Pacific Ocean
Centrobranchus brevirostris			+
C. choerocephalus			+
C. nigroocellatus	+	+	
C. andreae	+		+
Gonichthys cocco	+		+
G. barnesi			+
Hygophum hygomi	+	+	+
H. proximum		+	+
H. reinhardti	+		+
H. hanseni	+	+	+
H. macrochir	+		
H. taaningi	+		
Lowina interrupta	+	+	+
L. rara	+		+
Myctophum asperum	+	+	+
M. aurolaternatum		+	+
M. nitidulum	+	+	+
M. spinosum	+	+	+
M. lychnobium		+	+
M. affine	+		
M. punctatum	+		
M. obtusirostre	+	+	+
M. phengodes	+	+	+
Symbolophorus boops		+	+
S. californiensis			+
S. evermanni		+	+
S. rufinus	+	+	
Tarletonbeania crenularis			+

Table 21.3

Slope water species of potential commercial interest in the Atlantic, Indian and Pacific Oceans

Species	Atlantic Ocean	Indian Ocean	Pacific Ocean
Gonostomatidae			
Maurolicus muelleri	+	+	+
Myctophidae			
Benthosema pterotum		+	+
B. fibulatum		+	+
Diaphus watasei		+	+
D. coeruleus		+	
D. suborbitalis		+	+
D. burtoni *			+
D. umbroculus *			+
Lampanyctodes hectoris	+	+	+
Notoscopelus japonicus **			

* Reported only from the Southeast Asian Seas

** Endemic to the Oyashio-Kuroshio transitional area off Japan

Non-migrants: Most species of the genus *Cyclothone* and some of the genus *Gonostoma* (Gonostomatidae) do not make diel vertical migrations, remaining in the mesopelagic zone. The same might be true of some myctophid species of the genera *Electrona* and *Taaningichthys*. Non-migrants do not form dense schools and show a rather even distribution in a certain layer characteristic of the species. Frequency of occurrence and quantities caught have been high in micronekton net samples due to their sluggish swimming behaviour. At present the fishes of this group, from a fishery point of view, can be regarded as the least interesting mesopelagic species because of their deep habitat and dispersed distribution. The high wax content of most species of this group (Table 3.1) should also be recalled.

21.4 Present catches

At present there is little fishing for mesopelagic species. Off South Africa a myctophid fish *Lampanyctodes hectoris* has been caught in the purse seine fishery directed mainly toward the anchovy. The catches have fluctuated greatly (Table 21.4); the largest was about 42 000 tonnes, taken in 1973 (Newman, 1977). The gear used is purse seines, generally 20 - 35 fathoms deep, i.e. with an effective fishing depth of about 30 - 50 m (Newman *et al.*, 1978). The fish has been used for meal and oil production.

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Table 21.4

Catches of lanternfish off South Africa
Data from FAO Yearbook of Fishery Statistics
for 1977 and Centurier-Harris (1974)

Year	Catch tonnes
1969	1 134
1970	18 198
1971	2 600
1972	15 200
1973	42 400
1974	316
1975	87
1976	132
1977	5 650

A questionnaire sent out by FAO shows that Soviet vessels catch myctophids off West Africa (W. Fischer, pers. com.), but no further information on size of catch or species composition is available.

Off southeast Australia mesopelagic fish (mainly *Maurolicus muelleri* but also *Lampanyctodes hectoris*) have been caught during experimental fishing. So far the catches have been small, but the prospects have been described as promising (Anon, 1977; 1977a).

Off Japan some *Diaphus* species are caught and consumed locally but they are not marketed (Kawaguchi and Shimizu, 1978).

22. NEEDS FOR FUTURE STUDIES

There are many important fields that need further studies and only a few of them can be treated here.

Those areas where there are indications of dense mesopelagic fish concentrations should be further surveyed in order to (1) obtain more reliable stock size estimates, and (2) monitor natural fluctuations in stock size. The most important areas in this context seem to be:

1. Arabian Sea
2. The Bay of Bengal
3. Northwest Africa
4. Southwest Africa
5. East coast of Central South America
6. Southeast Asian seas
7. Japan Sea
8. Transitional area between the Oyashio and Kuroshio
9. Subarctic area in the North Pacific
10. West coast of Central America and Peru

The subantarctic and antarctic regions and the waters around various sea-mounts remain to be investigated.

Adequate knowledge of life history is restricted to only a few species and should be acquired for other species, especially dominant species. Further work is needed to evaluate the daily growth ring for ageing mesopelagic fish. If it is proved reliable, more tropical species should be aged for growth and mortality studies.

Difficulties in the identification of mesopelagic fishes have caused considerable problems in community studies. Therefore, preparation of practical keys is required for species identification worldwide. Egg and larva surveys have been inadequate mainly due to the difficulties in identification, except in the California Current region. Further work on egg and larva taxonomy is needed to prepare practical keys.

Studies should be carried out to trace any stock-recruitment relationship in the most important mesopelagic fish species (e.g. *Benthosema pterotum, Diaphus dumerili, Lampanyctodes hectoris* and *Maurolicus muelleri*). The data needed are long time-series of abundance estimates and preferably also of egg/larva production. This study should be started while the stocks are unexploited, and it should be given high priority if a commercial fishery is initiated. Other aspects of reproductive biology, e.g. fecundity, spawning behaviour and egg and larval survival, also need further research.

The role of mesopelagic fishes in the marine ecosystem is still poorly understood. Studies on the feeding habits of important species should be carried out to find at which trophic level they feed and to estimate their consumption rate. It is also important to learn more about predation on mesopelagic fish. There is evidence that they may serve as forage for various fishes, cephalopods and marine mammals, but quantitative data are very few and at present it is not possible to account for what happens to the large mesopelagic fish production.

Better gears to catch mesopelagic fish are needed, both for sampling and for fishery purposes. Sampling gears must be quantitative and they should be designed to sample discrete depth layers. For commercial fisheries priority should be given to gears which can catch species coming up to the upper 100 m during the night. The South African fishery for lanternfish has shown that purse-seines can be used, but for most species trawls are probably better suited. Trials with small-meshed trawls, designed to catch krill, appear to be promising, but much research on design and operation techniques remains to be done. Some species (e.g. *Benthosema pterotum*) are also easily caught during the daytime, but this requires

advanced acoustical equipment to monitor the trawl depth relative to the fish concentrations. To catch non-migrant species and others which do not form dense concentration, trawls which can filter very large quantities of water are needed, or artificial means of concentrating the fish must be found. Probably these problems will not be easily solved in the near future.

For stock size estimation acoustic methods should be further improved. It is very important to get target strength measurements of the most important mesopelagic fish species, and it is also important to study further the relationship between resonant frequencies and size and species of fish.

For a rational utilization of mesopelagic fish stocks it will also be necessary to do research on the processing of the fish and on the marketing of the products. But these questions and the economic aspects which have been dealt with by Wijkström (1978), fall outside the scope of this report.

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